UNIVERSITE DU QUEBEC A MONTREAL

ÉVALUATION DE L'EFFET DES COUPES PARTIELLES SUR LES ARTHROPODES TERRICOLES DANS DES PEUPLEMENTS D'ÉPINETTE NOIRE SUJETS A LA PALUDIFICATION

MEMOIRE
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TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

Bien que l'aménagement forestier écosystémique basé sur les perturbations naturelles soit généralement proposé afin de poursuivre la récolte de la matière ligneuse tout en conservant la biodiversité, son efficacité doit être démontrée. Dans ce mémoire, je compare les assemblages de carabes et d'araignées retrouvés dans une chronoséquence de peuplements naturels d'épinette noire enclins à la paludification à ceux de peuplements de même type ayant subi des CPRS traditionnelles et des coupes partielles sensées reproduire ou conserver des structures de peuplements anciens. Les 1 618 spécimens de carabes (Coleoptera : Carabidae) et 11 628 spécimens adultes d'araignées (Araneae) totalisant 163 espèces qui sont inclus dans cette étude ont été récoltés par pièges-fosses lors des étés 2007 et 2008. Les deux taxons à l'étude ont montré des changements dans leurs assemblages lors du vieillissement naturel des peuplements, mais leur réponse aux traitements sylvicoles a été très différente. Pour les carabes, la coupe n'a pas eu d'effet remarquable. Ceci s'explique par l'effet important de l'épaisseur de la matière organique qui s'accumule avec le temps passé en absence de feu. Pour les araignées, les coupes ont favorisé des assemblages qui n'avaient pas d'équivalent dans la gamme de peuplements naturels utilisés comme référentiel. L'importance de la surface terrière pour les araignées et de la matière organique pour les carabes conduisent à proposer une modification des stratégies de coupe afin de mieux tenir compte de ces deux attributs forestiers dans l'émulation des perturbations naturelles. Dans une optique d'aménagement et de conservation par filtre brut, les coupes partielles pourraient être efficaces en étant pratiquées dans des peuplements productifs afin de laisser sur pied une surface terrière assez importante pour être représentative de celle des vieux peuplements de la mosaïque qui résulte des régimes de perturbations naturelles de la région.

Mots-clés :
arthropodes terricoles, araignées (Araneae), carabes (Coleoptera : Carabidae), filtre brut, chronoséquence, coupes partielles, CPRS, pessière noire.

INTRODUCTION

0.1 Les arthropodes de la forêt boréale et la foresterie

Au Québec, on peut dire que c'est dès 1937, avec la mise en place du Bureau d'entomologie du ministère des Terres et Forêts, qu'apparut le premier type d'investigations sérieuses des arthropodes forestiers (Dorais *et al.*, 1996). Sa mission se limitait essentiellement à protéger la ressource ligneuse contre les insectes. Depuis lors, presque la totalité des recherches sur les arthropodes en forêt boréale québécoise a été menée dans cette optique, en se concentrant principalement sur les espèces épidémiques en raison de l'impact économique direct qu'elles peuvent avoir sur la récolte du bois. Toutefois, peu d'études ont été menées afin de documenter les impacts de l'exploitation forestière sur les arthropodes. Il s'avère donc difficile d'apporter des éléments de réponse à ce sujet.

Ceci est aussi dû à l'important manque à gagner qui subsiste quant aux connaissances les plus fondamentales de la diversité des arthropodes en forêt boréale québécoise, notamment leur distribution naturelle à travers les peuplements des différents stades successionnels (Paquin et Coderre, 1997b, Pearce et Venier, 2006).

Bien que des recherches aient eu lieu dans la pessière noire à mousses québécoise concernant la relation entre les arthropodes terricoles (du parterre forestier) et les changements de leur habitat, elles restent peu nombreuses. Deux études se sont concentrées sur les effets à court terme du feu ou de la coupe totale sur les communautés d'arthropodes terricoles (Larrivée *et al.*, 2005, 2008; Saint-Germain *et al.*, 2005), mais aucune étude n'y a encore investigué d'autres types de récolte. Afin d'avoir une idée des changements d'arthropodes terricoles à long terme dans les peuplements naturels, Paquin (2008) a caractérisé les communautés de carabes le long d'un gradient d'âge de peuplements d'épinette noire (Paquin, 2008). Son étude a permis de démontrer que des peuplements monospécifiques

recelaient des communautés d'arthropodes différentes à des stades de succession différents mais n'incluait pas de variables autres que le temps depuis le dernier feu pour expliquer ces différences. Plus à l'est, Janssen *et al.* (2009) ont étudié la relation entre les coléoptères terricoles et volants et les structures forestières à différentes échelles mais n'ont considéré que la richesse spécifique des coléoptères. Ils ont néanmoins observé que le nombre d'espèces terricoles était favorisé par une plus grande hétérogénéité dans la composition des peuplements et des paysages (Janssen *et al.*, 2009).

Dans le reste du Canada, les efforts ont surtout été concentrés en forêt boréale mixte (Addison et Barber, 1997; Cobb *et al.* 2007; Duchesne *et al.*, 1999; Niemelä *et al.*, 1993; Paquin et Coderre, 1997a, 1997b; Spence *et al.*, 1996; Work *et al.*, 2004, 2010). La majeure partie des connaissances qui lient la foresterie et les arthropodes des forêts boréales résineuses provient des pays scandinaves comme la Finlande, autant pour les pratiques traditionnellement utilisées que les méthodes de sylviculture alternatives (Heliölä *et al.*, 2001; Huber et Baumgarten, 2005; Koivula, 2002a, 2002b; Koivula *et al.* 2002; Koivula et Niemelä, 2002, 2003; Martikainen *et al.*, 2006; Matveinen-Huju et Koivula, 2008; Niemelä, 1997; Niemelä *et al.*, 1988, 2007; Pajunen *et al.*, 1995 ; Pihlaja *et al.*, 2006 ; Siira-Pietikäinen *et al.* 2003; Sippola *et al.*, 2002). Un constat général qui ressort de toutes ces études est que les pratiques forestières affectent les communautés d'arthropodes. Des tendances plus précises émergent : 1) les sites de feu et de coupes totales montrent des différences dans les communautés d'arthropodes qu'ils recèlent, 2) les sites récemment perturbés sont plus favorables aux espèces de milieux ouverts et certaines généralistes, alors que 3) les espèces associées aux vieilles forêts ont tendances à être défavorisées et un long laps de temps peut s'écouler avant qu'elles ne réintègrent le milieu, et 4) des coupes avec de hauts pourcentages de rétention (plus de 70%) peuvent amoindrir ces effets. Les résultats concernant la diversité des arthropodes suggèrent donc que des modifications soient apportées au système d'aménagement actuel à des fins de conservation, notamment en ce qui concerne la rétention d'arbres dans les peuplements.

0.2 Conserver la biodiversité des forêts par l'aménagement écosystémique

Depuis 1995, la conservation de la biodiversité (la diversité des espèces, de leurs gènes et des écosystèmes qui leur sont associés) fait partie des objectifs prioritaires de l'aménagement forestier durable au Canada (Conseil canadien des ministres des forêts [CCMF], 1995, 2003). Au Québec, ceci a contribué à placer l'aménagement écosystémique au cœur de la réorientation du cadre de la gestion forestière qui est en cours (Livre vert, 2008 ; Rapport Coulombe, 2004).

On peut définir l'aménagement écosystémique comme étant :

> Une approche d'aménagement qui vise à maintenir des écosystèmes sains et résilients en misant sur une diminution des écarts entre les paysages naturels et ceux qui sont aménagés afin d'assurer, à long terme, le maintien des multiples fonctions de l'écosystème et, par conséquent, de conserver les bénéfices sociaux et économiques que l'on en retire (Gauthier *et al.*, 2008b).

Ce type d'aménagement s'appuie sur le concept de « filtre brut », qui stipule qu'il existe une ou quelques échelles écologiques auxquelles il est possible d'agir afin de conserver la vaste majorité de la diversité biologique et ce, à tous les niveaux organisationnels (Bergeron *et al.*, 1999; Hunter *et al.*, 1988; Lemelin et Darveau, 2006; Noss, 1987). Compte tenu qu'une énorme proportion de la biodiversité nous est inconnue, seul des considérations à grande échelle de conservation des écosystèmes et des paysages permettraient de préserver les composantes qui y sont associées (Franklin, 1993). Des mesures spécifiques appliquées « espèce par espèce » à plus petite échelle sont aussi compatibles avec l'aménagement écosystémique en représentant un filtre fin qui assure la conservation de certaines espèces pour lesquelles les mesures qui relèvent du filtre brut ne s'avèrent pas suffisantes (Gauthier *et al.*, 2008b; McLaren *et al.*, 1998; Rempel *et al.*, 2004; Soulé, 1994).

0.3 L'émulation des perturbations naturelles

Les perturbations naturelles ont été proposées comme base de l'aménagement forestier écosystémique (Angelstam, 1998 ; Attiwill, 1994; Bergeron *et al.*, 1999 et 2007; Bergeron et Harvey, 1997; Delong, 2002; Franklin *et al.*, 2002; Galindo-Leal et Bunnell, 1995; Gauthier *et al.*, 2008; Kuuluvainen, 2002; Leduc *et al.*,

2000). Ceci s'explique par la reconnaissance du rôle qu'elles exercent en tant que force majeure qui agit sur les forêts et qui contribue à leur durabilité (Attiwill, 1994). Un tel type d'aménagement vise la pratique d'activités sylvicoles qui engendreront, à l'échelle du peuplement et du territoire, des attributs forestiers qui se rapprochent de ceux de la forêt régionale non aménagée. Ceci relève du principe de conservation par filtre brut, car la biodiversité devrait mieux réagir face à des pratiques sylvicoles qui engendrent des conditions du milieu semblables à celles qui résultent des perturbations naturelles puisque la biodiversité présente sur le territoire est présumée y être adaptée (Attiwill, 1994). En effet, les coupes et les perturbations naturelles peuvent avoir un impact sur la disponibilité d'habitats de qualité car elle relève des principaux attributs forestiers affectés par les perturbations : la structure d'âge des peuplements, la composition de la forêt, l'agencement des peuplements, les îlots et peuplements résiduels dans les zones perturbées, les arbres résiduels vivants ou morts et la matière organique au sol (Gauthier *et al.*, 2008a). Pour que ce type d'aménagement s'avère efficace, l'acquisition de connaissances profondes sur les écosystèmes touchés est donc primordiale (Bergeron *et al.*, 2008).

En forêt boréale, les épidémies d'insectes et les incendies sont les principaux agents naturels de perturbations à grande échelle. Dans la portion occidentale du domaine bioclimatique de la pessière noire à mousses québécoise, bien que la tordeuse des bourgeons de l'épinette puisse avoir un certain effet sur l'évolution des peuplements, le feu représente de loin le facteur dominant qui influence les attributs forestiers à grande échelle (Morin *et al.*, 2008), où cette perturbation est reconnue comme étant bénéfique à la régénération des essences résineuses (Doucet *et al.*, 1996). Ce sont surtout de grands feux qui sont à l'origine du retour des nutriments vers le sol et de la régénération massive des peuplements de la pessière noire à mousses de l'ouest: la plupart résultent d'incendies de 1 000 à 100 000 hectares, bien que ces derniers soient beaucoup moins fréquents que les feux plus petits (Bergeron *et al.*, 2002, 2004).

Bien qu'un événement d'incendie ait des répercussions sur les peuplements touchés, son absence a aussi des conséquences, bien que moins spectaculaires à

court terme. Plusieurs types de forêts et composantes de la biodiversité tirent profit du long intervalle de temps qui peut exister entre deux perturbations importantes à un même endroit (Boudreault *et al.*, 2002 ; Harvey *et al.*, 2002). Avec le temps, en l'absence de feu, les forêts ont une tendance naturelle à aller vers des peuplements diversifiés et de classes de diamètres inégales pour devenir très complexes en fin de succession (Franklin *et al.*, 2002 ; Lähde *et al.* 1999). La pessière noire à mousses ne fait pas exception, mais celle de la ceinture d'argile montre certaines particularités qui ont le potentiel de s'avérer importantes pour la biodiversité (Simard *et al.*, 2008).

0.4 Le cas spécifique de la ceinture d'argile québécoise

Tout d'abord, dans la partie nord de la ceinture d'argile, plusieurs peuplements ne connaissent aucune réelle succession d'essences d'arbres lors de leur développement, mais plutôt une structuration par une succession de cohortes de la même espèce : l'épinette noire. Cette dernière se retrouve sous forme de grands massifs presque purs sur le territoire plat de la ceinture d'argile, alors qu'environ 88% de la forêt représente des peuplements d'épinette noire de différents âges (Bouchard, 2008 ; Harvey *et al.*, 2003).

De plus, les peuplements d'épinette noire de la ceinture d'argile sont sujets à un phénomène lent et graduel qui vient affecter leur évolution : la paludification. Ce phénomène se produit surtout sur des sols mal drainés propices à l'envahissement par la sphaigne (*Sphagnum* spp.) et où le climat le permet. En l'absence prolongée de feu, la matière organique s'accumule et ses propriétés font monter la nappe phréatique et tendent à rendre les conditions de croissance des jeunes arbres plus difficiles (baisse de la température du sol, du taux de décomposition, de l'activité microbienne et de la disponibilité des éléments nutritifs), ce qui engendre une baisse de la surface terrière à long terme (Fenton *et al.*, 2005 ; Lavoie *et al.*, 2005a, 2005b). La structure des peuplements très paludifiés peut même être moins complexe que celle des stades antérieurs, étant donné que les chicots, les débris ligneux au sol et les arbres vivants de gros diamètres se sont raréfiés avec le temps (Harper *et al.*, 2005).

0.5 Le régime naturel de perturbations et l'usage extensif de la coupe totale

L'aménagement équien, par le biais de la méthode de régénération par coupe totale sur de grandes superficies, a souvent été comparé au feu, qui laisse un couvert forestier vivant presque inexistant à court terme sur l'aire touchée (Doucet *et al.*, 1996). Il est maintenant reconnu que les deux types de perturbations diffèrent de façon importante à plusieurs niveaux (Cyr *et al.*, 2009; McRae, 2001). À l'échelle de la perturbation même, les legs structuraux représentent l'un des principaux écarts entre les perturbations naturelles et les méthodes de coupes (Franklin *et al.*, 2002, Leduc *et al.*, 2000). En effet, même après les feux les plus sévères, des tiges debout vivantes, moribondes et mortes forment des patrons d'îlots intacts et de zones partiellement et totalement brûlées qui représentent une diversité de structures rémanentes qui contribuera à celle du prochain peuplement (Harvey et Brais 2007 ; Franklin *et al.*, 2002 ; Lähde *et al.*, 1999; Leduc *et al.*, 2000). Ces éléments structuraux sont beaucoup moins présents dans les aires de coupes totales (Vaillancourt *et al.*, 2008), ce qui a de sérieuses implications pour la biodiversité, plus spécialement pour les espèces qui ont un lien étroit avec le bois mort (Drapeau *et al.*, 2003, 2009; Imbeau *et al.*, 2001; Potvin et Bertrand, 2004).

En plus de la sévérité des coupes actuelles qui n'est pas représentative de la gamme de variabilité des perturbations naturelles, il en va de même pour leur fréquence, leur intensité, leur taille et leur espacement (Bergeron *et al.*, 1999, 2007; Perron *et al.*, 2008). Avec la diminution du nombre de peuplements matures et âgés attribuée à l'usage extensif d'un aménagement de type équien en plus de celle occasionnée par le régime de feu naturel, on est en voie d'assister à un rajeunissement à grande échelle de la structure forestière boréale, alors qu'on observe naturellement une mosaïque diversifiée de peuplements équiens et inéquiens résultant de la variabilité des paramètres spatiaux et temporels associés au feu (Bergeron *et al.*, 1999 ; Gauthier *et al.*, 2008a). Ceci fait planer une menace sur la biodiversité associée aux peuplements matures et âgés de cette mosaïque (Drapeau *et al.*, 2003).

À titre de référence, la Finlande représente un cas typique où les opérations forestières intensives qui y ont été pratiquées pour longtemps sur presque la totalité du territoire (hormis quelques zones protégées) ont mené à une diminution de la quantité des peuplements anciens et à l'uniformisation de la structure forestière, qu'on tente maintenant de restaurer (Kuuluvainen, 2002). Cette disparition de l'hétérogénéité naturelle des forêts à petite et grande échelles expliquerait pourquoi plusieurs composantes des écosystèmes forestiers y sont menacées ou disparues, dont des espèces d'arthropodes liées au bois mort (Niemelä, 1997). Ceci donne un aperçu de l'effet que pourrait avoir à long terme la poursuite de notre mode actuel de gestion forestière sur la diversité biologique (Imbeau *et al.*, 2001) et démontre le besoin de développer et d'adopter de nouvelles pratiques forestières diversifiées (Bergeron *et al.*, 1999 ; Drapeau *et al.*, 2003). Toutefois, un aspect important doit être souligné : l'application de l'aménagement forestier écosystémique basé sur les perturbations naturelles doit être adaptée à chaque région et non prescrite à la forêt boréale de façon planétaire (Gauthier *et al.*, 2008b; Niemelä, 1997).

0.6 Un modèle d'aménagement forestier écosystémique

Bergeron *et al.* (1999) ont proposé un modèle d'aménagement écosystémique pouvant s'appliquer à différentes régions de la forêt boréale, dépendamment du cycle de feu et de l'âge de récolte maximale des peuplements. Toutefois, le cycle de feu peut être complexe à calculer et la moyenne d'âge des peuplements de la région qui en résulte peut s'avérer être un meilleur choix (Harvey *et al.*, 2002). Pour le sous-domaine de l'ouest de la pessière noire à mousses, la moyenne d'âge des peuplements issue des régimes passés et présent de perturbations se situe autour de 136-140 ans sur les sols argileux et organiques (Bergeron *et al.*, 2004), et l'utilisation exclusive de coupes totales tend à faire baisser cette moyenne.

Le modèle des trois cohortes qu'ont présenté Bergeron *et al.* en 1999 a évolué depuis lors (Bergeron *et al.* 2002 ; Bouchard, 2008 ; Harvey, *et al.*, 2003), mais il vise toujours à diversifier les méthodes de coupes afin de reproduire et de conserver les différents types de peuplements dans des proportions se rapprochant

de celles issues du régime de perturbations naturelles d'une région tout en poursuivant la récolte de la matière ligneuse (Gauthier *et al.*, 2008a). Dans ce modèle, les coupes totales visent encore à imiter les feux en retrouvant des peuplements équiens en régénération de cohorte I, alors que les coupes partielles et sélectives recèlent le potentiel de conserver et de reproduire de manière accélérée les structures plus complexes des peuplements de cohortes II et III qui résultent d'une absence prolongée de feu. En effet, les coupes partielles constituent un prélèvement d'arbres qui diminue la surface terrière du peuplement et crée une ouverture accrue de la canopée tout en maintenant un couvert forestier, comme le ferait la paludification sur plusieurs années.

Aussi, le modèle de Bergeron *et al.* (1999) montre que les coupes totales peuvent s'insérer dans un système d'aménagement écosystémique, bien que certaines modifications à son utilisation soient nécessaires pour entrer dans la gamme de variabilité naturelle des attributs forestiers (Leduc *et al.*, 2000 et voir sect. 0.5 ci-haut). Ainsi, selon la notion de filtre brut, le modèle des trois cohortes pourrait assurer la conservation de la majorité de la biodiversité associée à ces stades de succession (Begeron *et al.*, 1999; Boudreault *et al.*, 2002). Toutefois, le concept théorique du filtre brut reste encore à vérifier expérimentalement (Rempel *et al.*, 2004) et les études concernant l'efficacité écologique d'un aménagement de type inéquien sont limitées (Le Goff et Bergeron, 2005), même si des progrès ont été réalisés ou sont en cours (Fenton *et al.*, 2008).

0.7 Réseau d'expérimentation de coupes partielles de l'Abitibi (RECPA)

Au Québec, le Réseau d'expérimentation de coupes partielles de l'Abitibi (RECPA) est un projet d'envergure mené conjointement par des chercheurs et des compagnies forestières de cette région (Fenton *et al.* 2008). D'autres projets semblables ont vu le jour en forêt boréale canadienne (Harvey *et al.*, 2008 ; Spence et Volney, 1999) et leurs caractéristiques les mettent au cœur des étapes nécessaires vers la mise en œuvre de l'aménagement écosystémique (Bergeron *et al.*, 2008). Pour le RECPA, plusieurs secteurs expérimentaux de différents traitements sylvicoles ont été mis en place dans l'optique d'évaluer l'efficacité

économique (coûts d'opération et productivité forestière) et écologique de la coupe partielle dans la pessière à mousses de la ceinture d'argile du Québec et de l'Ontario (Fenton *et al.*, 2008).

Certains objectifs spécifiques du RECPA rejoignent directement la notion de filtre brut en voulant évaluer en quoi les coupes partielles permettent de recréer ou de maintenir une structure de peuplements qui s'apparente à celle des peuplements surannés et anciens des mosaïques naturelles et d'évaluer les effets de ces pratiques sylvicoles sur la biodiversité (Fenton *et al.*, 2008).

Ceci représente d'ailleurs l'essence de mon projet, en ciblant tout particulièrement les arthropodes terricoles. Ces derniers, comme les carabes et les araignées, sont reconnus pour avoir un bon potentiel en tant que bioindicateurs écologiques (voir la revue de littérature sur le sujet par Pearce et Venier, 2006), même s'ils ne font pas tous l'unanimité. En effet, une certaine controverse existe quant à leur pouvoir de jouer ce rôle présentement à cause de la nécessité de choisir des espèces en particulier et d'améliorer les connaissances sur les taxons les plus étudiés (Langor et Spence, 2006 ; Thompson, 2006). L'utilisation d'indicateurs fait d'ailleurs partie des objectifs spécifiques du RECPA (Fenton *et al.*, 2008) et fait aussi partie des orientations vers lesquelles se dirige le nouveau système de gestion des forêts au Québec (CCMF, 2003 ; Livre vert, 2008). Ils devraient autant servir dans la planification des opérations que le suivi environnemental ensuite (Kneeshaw *et al.*, 2000 ; Rempel *et al.*, 2004).

Par les deux volets qu'il comporte, il est raisonnable d'affirmer que mon projet de maîtrise contribuera à l'élaboration de l'aménagement écosystémique en faisant directement partie de deux des cinq étapes nécessaires à sa mise en œuvre selon Bergeron *et al.* (2008).

0.8 Volet 1 : les arthropodes et la dynamique naturelle des peuplements

La reconstitution de l'évolution à long terme des peuplements après perturbation s'insère dans la première étape par laquelle il faut passer pour arriver à un aménagement écosystémique (Bergeron *et al.*, 2008). En ce sens, le premier volet de mon projet consiste à caractériser les communautés d'arthropodes

(carabes et araignées) terricoles de peuplements matures et âgés d'épinette noire sujets à la paludification. Ces peuplements diffèrent selon leur âge (93 à 288 ans) et forment une chronoséquence qui vise à représenter les différents stades avancés de la succession propre à la région à l'étude. L'approche par chronoséquence, ou la « substitution du temps par l'espace », a déjà fait l'objet de critiques (Johnson et Miyanishi, 2008), mais elle est tout de même vue comme un bon moyen d'accroître nos connaissances concernant l'évolution des peuplements à long terme (Groot *et al.*, 2005).

Paquin (2008) a déjà décrit les changements de communautés de carabes en fonction du temps après perturbation dans la même région. Cependant, mon étude inclut aussi les araignées terricoles, qui y sont beaucoup plus abondantes et diversifiées. Ces deux caractéristiques pourraient s'avérer importantes afin d'augmenter la détection des changements structuraux des peuplements à l'étude (Langor et Spence, 2006 ; Pearce et Venier, 2006), étant donné qu'il n'y a pas de réelle succession d'essences forestières avec le temps (Harper *et al.*, 2005) et que l'influence de la composition forestière sur les arthropodes est importante (Paquin et Coderre, 1997a). Ainsi, en pessière noire à mousses de la ceinture d'argile, la structuration des peuplements devrait jouer un rôle particulier pour la biodiversité (Simard *et al.*, 2008).

Harper *et al.* (2005) ont établi une classification des divers stades successionnels de la région en mettant en relation l'âge des peuplements et des mesures de leurs éléments de structures (arbres vivants, chicots et bois mort au sol). Leurs classes pourraient donc se refléter sur les communautés d'arthropodes terricoles, ce qui aiderait à évaluer la pertinence de préserver ou de recréer tous les stades de la succession pour la conservation de ces organismes. Ainsi ce volet de mon projet agit à titre de système naturel de référence et est complémentaire au Volet 2 de mon projet.

0.9 Volet 2 : les arthropodes et les coupes partielles

Le deuxième volet de mon projet rejoint les préoccupations écologiques qui ont mené à la mise en place du RECPA en termes de diversité biologique (voir plus haut sect. 0.7) en ciblant particulièrement les arthropodes terricoles.

Son but est d'utiliser les sites du RECPA pour l'échantillonnage des arthropodes terricoles non seulement pour investiguer leurs réponses face aux traitements sylvicoles, mais également pour comparer leurs communautés à celles de la chronoséquence. Mon étude contribue donc à la deuxième étape menant à la mise en œuvre de l'aménagement écosystémique, en faisant une analyse comparative des paysages naturels et des paysages aménagés et en y identifiant les principaux écarts (Bergeron *et al.*, 2008). Ces écarts entre les communautés d'arthropodes terricoles des différents milieux devraient être dus, selon le principe de filtre brut, aux écarts dans les éléments structuraux d'habitat des peuplements traités et naturels. Ainsi, les peuplements traités par coupe partielle devraient receler des communautés d'arthropodes plus semblables à celles des peuplements plus âgés de la chronoséquence si leur structure l'est aussi.

0.10 La structure du document

Les deux volets de mon projet seront traités ensemble dans chacun des deux chapitres qui suivent. Le Chapitre I traitera des carabes, alors que le Chapitre II traitera des araignées. La conclusion témoignera des différences entre ces deux taxons se retrouvant en pessière noire à mousses et des implications de ma recherche pour l'aménagement écosystémique et la conservation de la biodiversité.

CHAPITRE I

RESPONSE OF GROUND BEETLES (COLEOPTERA : CARABIDAE) TO ADAPTED PARTIAL CUTTING AS A COARSE FILTER APPROACH IN BLACK SPRUCE STANDS PRONE TO PALUDIFICATION

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1.1 Abstract

In this chapter, I use ground-beetles (Coleoptera: Carabidae) to evaluate whether partial cutting and a cohort model of ecosystem management are sufficient to preserve biodiversity found in the mature and old-growth black spruce stands of the northern Clay belt in Québec (Canada). I compared carabid fauna in partial cuts, clear-cuts (CPRS) and uncut control stands with a chronosequence of mature and old naturally regenerated stands (94-288 years since the last fire). Responses in carabid assemblages suggest that partial cutting in younger, more closed stands could create stand conditions consistent with old-growth for carabids. These conditions can however be maintained in older stands whether they were cut by CPRS or partial cutting and these treatments did not seem to change or add pertinent habitat elements of structure for carabids. I attribute the lack of apparent effect of CPRS and partial cutting on carabid communities mostly to the conditions of the stands prior to cutting, namely the omnipresence of the moss layer, which is preserved by the cutting methods. Coarse filter approaches for this region should thus include forest floor thickness as an important stand feature for biodiversity in addition to retained basal area because of its role for biodiversity and stand dynamics. According to our results, maintaining the thick organic layer of old stands would favour communities of carabids consistent with old stands.

1.2 Introduction

Coarse-filter conservation, whereby habitat is maintained in the hope that a large proportion of associated species will in turn be protected, is often advocated as an effective and viable means of preserving species on managed landscapes (Bergeron *et al.*, 1999; Franklin, 1993; Galindo-Leal and Bunnel, 1995; Lemelin and Darveau, 2006; Noss, 1987). In the boreal, this approach relies on the assumption that species evolved under long-term selection facing natural disturbances (Hunter, 1990) and thus could be preserved by silvicultural methods that recreate forest attributes including stand-age structure and forest composition in a mosaic consistent with natural disturbances (Attiwill, 1994; Franklin, 1993; Gauthier *et al.*, 2008a, 2008b). This approach, also termed natural-disturbance based management (NDBM), has become the cornerstone of ecosystem management in boreal forests (Bergeron and Harvey, 1997; Gauthier 2008b, Hunter 1990). While enticing in its simplicity, NDBM must be adapted to the peculiarities of a given region rather than applied as a one-size fits all prescription throughout the boreal as disturbance dynamics, ecosystems and biodiversity vary across the landscape (Gauthier *et al.* 2008b; Larue *et al.* 1996; Niemelä, 1997; Noss, 1999; Noss *et al.*; 2002; Work *et al.*, 2003).

While insect defoliation and large scale windthrows affect successional dynamics in black-spruce stands (*Picea mariana* Mill.) within the Clay belt region of northwestern Québec, Canada, (Morin *et al.*, 2008; Simard *et al.*, 2008), stand-replacing wildfire remains the principal natural disturbance determining in large part forest composition (Bergeron *et al.*, 2004; Gauthier *et al.*, 2000; Simard *et al.*, 2008). The disturbance regime in this area has resulted in a mean stand age of 148 years with more than half of the stands (57%) present as older than the cutting rotation age (100 years) (Bergeron *et al.*, 2004; 2001). As forests tend towards diversification with more complex structures with time (Franklin *et al.*, 2002; Lähde *et al.*, 1999), old black spruce stands are thought to be important for maintaining species that benefit from long intervals between disturbance events (Boudreault *et al.*, 2002).

Unlike mixedwood stands, black spruce stands show little compositional change in terms of tree species with time since fire (TSF) on poorly drained soils of the Ontario-Québec Claybelt. Rather, these stands develop structural complexity (described by Harper *et al.*, 2005) through a succession of single species cohorts of black spruce. Stand development begins when regenerating black spruce establishes as an even-aged cohort following wildfire. With time, these trees form stands with closed canopies characteristic of the stem-exclusion stage. This structurally simple stage persists approximately 100 years until basal area decreases and dead wood inputs increase with the concurrent break-up of the canopy caused by natural tree mortality (Harper *et al.*, 2005; Lecomte *et al.*, 2006). A second cohort of black spruce can initiate following mortality within the first cohort. The stand thus transitions from a simple, even-aged to a more structurally complex stand (Harper *et al.*, 2005). Following understory reinitiation/tree growth stage, structural diversity and canopy opening continue to increase as stands become increasingly paludified. These conditions define 'old-growth' in these stand types (Harper *et al.*, 2005).

A key factor determining the structural complexity of these stands is paludification. Paludification is a slow and gradual process occurring on poorly drained soils prone to *Sphagnum spp.* invasion, which promotes organic matter accumulation and reduces tree growth (Fenton *et al.*, 2005; Lavoie *et al.*, 2005a, 2005b). This process ultimately leads to reduced structural diversity in old growth stands with trees, snags and logs with smaller diameters (Harper *et al.*, 2003; Harper *et al.*, 2005).

Bergeron *et al.* (1999) proposed a cohort-based model of forest management meant to maintain the diversity of stand structures consistent with stand development observed in uncut black-spruce forests in this area. While this model has been modified (Bergeron *et al.*, 2002; Bouchard, 2008; Harvey, *et al.*, 2003), it still includes elements of clearcutting meant to create even-aged / regenerating stands and partial cutting meant to maintain or recreate stand structures similar to those observed in older black-spruce stands. In mature stands, stems are removed through partial cutting to emulate lower basal area and

related opening canopy associated with natural old-growth black spruce stands. Under the coarse filter approach, this cohort model should maintain species assemblages within partial cut stands similar to those found in old forests, where the structural heterogeneity is expected to be of special interests for biodiversity (Simard *et al.*, 2008).

Like any proposed management strategy, the success of the cohort model to preserve biodiversity must be verified experimentally (Drapeau *et al.*, 2008; Rempel *et al.*, 2004). Bergeron *et al.* (2008) underline knowledge about long term stand development following disturbance and identification of the major differences between natural and managed landscapes as two initial and necessary steps towards the implementation of ecosystem management. Comparison of the response of biodiversity to natural disturbance regimes and forestry practices is thus a logical way to measure the ecological efficiency of these practices.

Many studies have been conducted regarding the effects of forestry practices on ground beetles (Coleoptera: Carabidae) in boreal forests. These organisms have been utilised as indicators of the success or failure of forest management practices such as clear-cutting, retention-felling and thinning because they are abundant, diverse and readily respond to environmental changes (see reviews by Koivula and Niemelä, 2002; Pearce and Vanier, 2006; Rainio and Niemelä, 2003). These studies indicate that ground beetles respond rapidly to intensive cutting, with forest species being replaced by open-habitat specialists and generalists. Conversely, less intensive harvesting like thinning and partial cutting with high retention (> 50%) show almost no negative effects on ground beetle communities (Koivula and Niemelä, 2002; Work *et al.*, 2010). In eastern black spruce forests, two recent studies investigated the response of carabids to forest succession (Paquin, 2008), wildfires and traditional harvesting methods (Saint-Germain *et al.*, 2005). Paquin (2008) found carabid succession followed stand development, as certain species were more abundant in newly disturbed habitats while others showed greater affinity for particular successional stages, showing that age of these monospecific stands inflenced structure of carabid communities. In cut and naturally burned stands, Saint-Germain *et al.* (2005) demonstrated that carabid

assemblages in clearcuts were more similar to uncut stands than to burnt areas and attributed this difference to numerous remnant populations in clearcuts that were present before cutting. Taken together these studies suggest that clearcutting is not equivalent to fire for biodiversity and that every stage of forest development may have unique arthropod compositions or even unique species that could be considered when conservation issues are involved. However, none of these studies have addressed alternative harvesting methods in this area, particularly the role of partial cutting.

In this chapter I test the efficacy of the cohort model as a viable coarse filter approach for preserving biodiversity in black spruce stands prone to paludification by monitoring changes in ground-beetle assemblages. A necessary initial step in the verification of the cohort model is the elaboration of changes in beetle assemblages along a time since fire (age) gradient. I expect ground beetle assemblages to undergo gradual changes with stand maturation, with species benefiting from increased structural diversity in old stands while other species would be disadvantaged by the decrease in basal area that accompanies paludification in this region of the boreal forest of eastern North America. Characterising beetle assemblages along this chronosequence of stands will serve as a series of reference stands whereby I can evaluate if partial cutting is effective at maintaining biotic communities consistent with older, more structurally complex stands.

1.3 Material and methods

1.3.1 Study area

My study area is located on the northern portion of the Abitibi Clay belt in north-western Québec (Canada) (49° 00'-50° 00'N; 77° 30'-79°0 8'W, Elevation: 256-314m) (Figure 1.1). This geophysical unit extends into Ontario and covers *ca.* 125 000 km^2 (Lefort *et al.*, 2002). The region is flat ranging from 255 and 280 m in elevation and characterized by heavy clay soils and till. Daily average temperatures at La Sarre, Amos and Matagami (Figure 1.1) are respectively 0.7, 1.2 and -0.7 °C and average annual precipitations are of 889.8, 918.4 and

905.5mm (Environment Canada, 2005). These characteristics make the stands of the region unde study prone to paludification (Lavoie *et al.*, 2005a, 2005b).

This region is part of the black spruce-feather moss bioclimatic domain (Bergeron *et al.*, 1998) which covers about 28% of the province of Québec and represents an economically important source of wood. Stands in this region are dominated by black spruce (*Picea mariana* Lamb.). Other tree species do occur but represent a minor component of the landscape and are principally found only in early serial stages. The herb layer is dominated by ericaceous species (Fenton *et al.*, 2007). Lichens are common but bryophytes are omnipresent: exposed mineral soil is rare, rather mosses occupy most of the ground layer (*Pleurozium shreberi*, *Dicranum polysetum*, *Hylocomium splendens*, *Ptilium cristacastrensis* and various *Sphagnum* species) (Fenton *et al.*, 2007). In some cases, moss mats can be more than 1.5 meters thick, especially in old stands originating from low severity fires (Fenton *et al.*, 2005).

1.3.2 Chronosequence

I sampled ground-beetles from 9 stands (see Table 1.1 and Figure 1.1) within a chronosequence of stands that vary in age from the last major fire (Bergeron *et al.*, 2001; Boudreault *et al.*, 2002; Fenton *et al.*, 2005; Lecomte, 2005). Stand structure along this time-since-fire (TSF) gradient can be characterized, according to Harper *et al.* (2005), by four major phases of development after stand-replacing fire: stand initiation (0-34 years), stem exclusion (34-96 years), understory reinitiation (96-164) and old-growth (> 164 years). (see the introduction for more details).

In these stands, age was determined using dendrochronology by N. Fenton *et al.* (2005) and C. Boudreault *et al.* (2002). However, tree ring estimates may underestimate the actual time since the last fire. For example, Lecomte *et al.* (2006) estimates the oldest site (288 years old) to be over 700 years old using radiocarbon-dating. However, not all sites have been carbon-dated and stand ages based on tree-rings still provide a means to make relative comparisons and inferences regarding stand development. Organic matter data and stand basal area

were provided by Fenton *et al.* (2005). Downed coarse woody material (CWM) and finer-scale estimates of basal area (20m x 20m plots) were measured by J. Jacobs (*unpublished data*) in the summer of 2008. For CWM, two star plots were established in each stand (Ståhl *et al.*, 2001) consisting of three 20 m transects radiating from a common midpoint (the center of our experimental plot) and separated by 120 degrees. For each intersected piece of CWM larger than 5 cm in diameter, the exact diameter and the decay class were recorded using a five class system (modified from Maser *et al.*, 1979). Stand level volumes were computed using the Van Wagner (1968) formula.

1.3.3 RECPA (Réseau d'expérimentation de coupes partielles de l'Abitibi)

In addition to the chronosequence sites, I sampled beetles from 4 replicated blocks (sectors) of the RECPA partial cutting network (Table 1.1). The RECPA (Réseau d'expérimentation de coupes partielles de l'Abitibi) consists of a total of 11 experimental sectors, which comprise complete replicate sets of CPRS, partial cutting and uncut stands. RECPA is a collaborative project between TEMBEC, Scierie Landrienne, Domtar, Abitibi-Bowater and the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management. A specific objective of the RECPA project is to determine if partial cutting can recreate or maintain stand structure that resembles that of the old-growth and ancient stands characterising the natural mosaic of the region (Fenton *et al.*, 2008). The initial experimental sector was established in 1998 with successive sectors being added, creating an additional temporal gradient of time-since-harvest implicit in my sampling.

I used four sectors (Cramolet, Fénélon, Gaudet and Puiseaux) within 120 km of each other (Figure 1.1). Stands from these sectors were between 100 and 300 years old before harvest (see Table 1.1) and were allocated to 3 treatments: 1) controls (untouched stands representative of the stands before logging); 2) partial cutting with variable retention (2 to 75% of basal area retained, see Table 1.1) and 3) CPRS (French acronym meaning "logging with protection of advanced regeneration and soils"). CPRS is the most commonly used harvesting practice on the Clay belt (Lefort *et al.*, 2002) where tree removal can be > 99% and skid trails

resulting from machinery activity are limited to ≤ 25% of the forest floor to minimize impacts on soils and small stems from harvesting machinery. An exception is in Cramolet, where scarification was applied in 2008 throughout the CPRS stands to mix organic with mineral soils. Permanent sampling plots were established in all treatments of each sector following the standards of the Ministère des Ressources naturelles et de la Faune (Direction des inventaires forestiers du Québec, 2006) for long-term monitoring of trees, vegetation and soil before and after cuts. Environmental data for RECPA stands was supplied by the RECPA project (unpublished data).

1.3.4 Beetle sampling

I sampled beetles during the summers of 2007 and 2008. Within each chronosequence stand, 2 sampling stations were installed. Within each of the 4 RECPA sectors (Cramolet, Fénélon, Gaudet and Puiseaux) 3 sampling stations were installed in association with RECPA's permanent sampling plots already existing each in control and CPRS stands. In partial cuts, I used a total of 6 stations (3 in low retention areas and 3 in high retention areas) to sample the gradient of retention left within this treatment. In Cramolet, low and high retention were respectively 1/3 and 2/3 retention areas inherent to sector's design. Each trap plot consisted of 3 pitfall traps placed in a triangle where each trap was placed 5-10 meters from the center. Pitfall traps (either 295 or 355 millilitres plastic cups but always with the same opening diameter of 8.5 cm) were positioned at the forest floor surface or slightly below the moss layer. All traps were covered with a supported rain guard (10 x 10 cm) made of white corrugated plastic (COROPLAST®). The rain guard was raised above ground level with two metal wires permitting the capture of epigaeic arthropods. Excess rain was allowed to escape through a paired internal cup system to minimize trap flooding. Within each trap, 25-30 ml of propylene-glycol (Prestone LowTox® Antifreeze/Coolant (AF/C), Mississauga, ON) was added as a preservative. Traps were installed between May 5-12 in 2007 and between May 8-12 in 2008. Traps were serviced at c. 3 week intervals with final collections being made between

September 12-16 in 2007 and August 12-17 in 2008. Undergraduate students and I sorted all samples into three groups; carabid beetles, other coleoptera and spiders. All specimens were stored in 70% ethanol.

I then identified mature carabid specimens at the species-level using taxonomic keys developed by Carl Lindroth (1961, 1963, 1966, 1968, 1969a and 1969b). Nomenclature follows Bousquet (2004). Sex was also determined for each specimen but was not used in the analyses.

1.3.5 Data analysis and statistical approaches

I used individual-based rarefaction curves to evaluate whether sampling was sufficient to adequately characterize species assemblages within only uncut forests, only cut stands, and both combined. Rarefaction curves were determined using the vegan package (Oksanen *et al.*, 2006) in R version 2.4.0 (R Core Development Team, 2006). Note that all further statistical analyses were also done using this software.

I standardized carabid abundances to daily catch-rates by dividing the number of individuals summed at the stand level by the number of active trapping days. These catch-rates are used in all further analyses at the stand level to allow for stand level conclusions relevant to the coarse filter approach and to forest management. Various transformations attempts were applied to the data but none were retained unless mentioned.

To characterize carabid response to natural stand dynamics, I used all uncut stands, or all stands used in the Chronosequence study and uncut control stands from REPCA project.

I used non-metric multidimensional scaling (NMDS) to characterize carabid assemblages as it avoids certain excessive statistical assumptions that may be ecologically unsupported or unwarranted (McCune and Grace, 2002). Ordinations were based on Bray-Curtis distance as this measure eliminates shared 'absences' or 'double zeros' which would otherwise be treated as a positive measure of assemblage similarity between sites (Legendre and Legendre, 1998) and is relatively more sensitive to responses of rare species than Canberra-metric

distance. I used "bestnmds" function in the vegan library (Oksanen *et al.*, 2006) for all ordination procedures. In these analyses, I used 40 random starting configurations each with up to 100 iterations (minimizing the risk of the iteration falling into a local minimum) to find the lowest stress solution.

I used pair-wise multi-response permutation procedures (MRPP) with Bray-Curtis distance and based on 4999 permutations (*mrpp* function from *vegan* library, Oksanen *et al.*, 2006) to test for significant differences between *a priori* groupings of the stands. *p* values and an associated chance-corrected within-group agreements (*A*) are given for every analysis. The latter (*A*) describes within-group homogeneity compared to what is expected by chance and varies from 0 (equals random heterogeneity within groups) to 1 (when all items within groups are identical). For all uncut stands, I tested *a priori* groupings corresponding to the structural stages proposed by Harper *et al.* (2005). I used three different stages: stem exclusion (34-96 years), understory reinitiation (96-164 years), and old-growth (>164 years). The Cramolet control site (100 years old) was placed in stem exclusion group because it is nearer to stands of this group in terms of age than to those within the understory reinitiation stage (133, 134 and 134 years old). I then compared harvested and control stands according to their treatment (CPRS, more and less intense partial cuts, controls) irregardless of the sector (Cramolet, Fénélon, Gaudet and Puiseaux). Finally, I grouped all the treated stands and compared them to the uncut stands as a group.

I used two complementary statistical methods to link characteristics of the stands with beetle assemblages. First, I used distance-based multivariate regression trees (dbMRT, De'ath, 2002) to compare beetle assemblages based on stand structural variables, age and time since disturbance (cut or fire). Again, Bray-Curtis distance was used. To understand how beetle assemblages changed with stand development, carabid assemblages were regressed against age of the stand (in years), total basal area ($m^2 \cdot ha^{-1}$), organic matter thickness (cm), and volume of total coarse woody debris as well as volumes of its 5 decay classes ($m^3 \cdot ha^{-1}$) using only uncut forests (see Table 1.1 for stand description). To understand the interaction between forest management and stand development,

beetle assemblages were regressed against the same covariates as the previous analysis (age of treated stands is their age before cut) while adding harvesting treatment, retention percentage, basal area prior to cutting ($m^2 \cdot ha^{-1}$) and time since the last disturbance (cut for treated stands and fire for regenerated stands) as covariates (again, refer to Table 1.1). Final tree size was chosen based on cross-validation and consensus based on 1000 trees: the most frequently chosen size of tree relative to its lowest cross-validated error is kept. According to De'ath (2002), the cross-validated error is supposed to vary from 0 (perfect predictor) to 1 (poor predictor). dbMRT were performed using the "mvpart" function from the library of the same name (De'ath, 2006).

I used indicator species analyses (Dufrêne and Legendre, 1997, "duleg" function from "labdsv" Roberts, 2006) to identify species characteristic of each terminal node of the dbMRTs. In this type of analysis, the indicator value (IndVal) is the product of the relative frequency and the relative abundance of a single species to give a measure combining species fidelity (present in all the sites of a group) and specificity (present in one group in particular) for a group of sites. I used 40 % or greater values as representative of strong indicator species, as supported by Buddle *et al.* (2006) and Work *et al.* (2004).

The second method I used to link stand variables with beetle assemblages is the Mantel test (vegan library from Oksanen *et al.*, 2006), which tests linearity of the changes among stand variables and beetle assemblages. Like MRT, Mantel test is a non-parametric test but instead of working as constrained clustering (De'ath, 2002), it tests whether there is a linear relationship between two different distance matrices of the same objects (Legendre and Legendre, 2008) (for example between the dissimilarity of the carabid assemblage between stands and the dissimilarity of each value of environmental variable characterising these stands). In our case, this is pertinent since many stand characteristics show a linear relationship with time since fire (Fenton *et al.*, 2005). The strength of relationship (r) between the matrices is called in this context the Standardized Mantel statistic (McCune and Grace, 2002). The distance measures used for this test were Bray-Curtis for beetle assemblages and Euclidean for every stand

variable, as double zeros in stand characteristics are meant to count for the similarity between stands, but not for beetles, since a species can be absent from two places (double-zeros) that are totally different (an extreme exemple would be a desert and a lake). I judge MRT to be more appropriate to depict break points in carabid assemblages like the different successionnal stages from Harper's model (2005) but also to be less efficient to show gradual, linear changes in the carabid assemblages associated to linear changes in their environment. In our case, both are interesting and thus both methods (dbMRT and Mantel test) will be used.

I also used linear regressions to investigate catch-rates of individual species with stand age. Analyses for individual beetle species were done with the "lm" function. Also, to investigate possible punctuated changes for species related to punctuated stand changes as described in the cohort model (Harper *et al.*, 2005), I used Student's T test to compare individual species catch-rates between successional stages. These two parametric tests were applied only when the required assumptions of normality and homoscedasticity were met. To meet these assumptions, McCune and Grace (2002)'s modified log-transformation for small numbers was used:

$$b_{ij} = \log\left(x_{ij} + d\right) - c\,,$$

where: c = order of magnitude constant = Int(log(Min(x)));

d = decimal constant = log-1 (c);

Min(x) is the smallest nonzero value in the data;

Int(x) is a function that truncates x to an integer by dropping digits after the decimal point.

This transformation avoids negative values resulting from log-transformation of catch-rates between 0 and 1 while keeping them equal to 0 after the transformation when they are 0. Adding 1 to every value of a dataset is the traditional way to deal with zeros with log transformations, but in our case 1 is too high compared to the lowest catch-rates and would tend to eliminate differences between small values (McCune and Grace, 2002).

1.4 Results

1.4.1 General

I caught 1 618 individual carabids (836 and 782 in uncut and cut stands respectively) representing 27 species over total 37 889 trap days (Annex and Figure 1.2). Sixteen species were represented by 5 individuals or less (See Annex). Trapping effort was sufficient to characterize ground-beetle richness in our study area as rarefaction curves approached asymptote (Figure 1.2). Trapping effort was more intense in treated stands compared to uncut stands largely due to the additional traps in partial cutting treatments (22 345 and 15 544 trap-days respectively). Catch-rates were higher in uncut stands than in treated stands (0.054 and 0.035 beetles/trap-day respectively). Five species were only collected in uncut forests compared to 12 species collected only in treated stands.

Five abundant species accounted for 89.4% of the total catch and were, in decreasing order, *Pterostichus adstrictus* Eschscholtz, *P. punctatissimus* (Randall), *Scaphinotus bilobus* (Say), *P. coracinus* (Newman) and *Platynus decentis* (Say). These species had the same rank order of abundance in uncut stands and accounted for 93.4% of the carabid abundance. In cut stands, they represented 85.0% of the abundance and only *Pterostichus coracinus* and *Platynus decentis* interchanged ranks.

1.4.2 Changes in ground-beetle assemblage with natural stand development

A two-dimensional NMDS ordination (stress = 7.68) characterized carabid assemblages with axis 1 reflecting a gradient in stand development (Figure 1.3). Based on winthin chance group agreement (A) of the MRPP, carabid assemblages in old-growth stands were more similar to understory reinitiation stage (MRPP, A = 0.127, p = 0.0168) than to stem exclusion (MRPP, A = 0.2944, p = 0.0088). However, carabid assemblages did not conform to the early phases of stand structural development proposed by Harper *et al.* (2005), as stands from stem exclusion and understory reinitiation were not different (MRPP, A: 0.01133, p = 0.305). Taken both as a group, they were still different from old-growth (MRPP,

A = 0.2252, $p < 0.0002$). Mantel tests (Table 1.4) revealed that changes in carabid composition were linearly related with changes in stand age (Mantel r = 0.373, p = 0.011), organic matter thickness (Mantel r = 0.479, $p < 0.001$) and stand basal area (Mantel r = 0.465, $p < 0.001$).

I observed a two node dbMRT (chosen 982 times out of 1000) relating carabid assemblages to descriptive variables (Figure 1.4). The single split was attributed to stand age (158.5 years) and separated old growth stands from stem exclusion and understory reinititation, explaining 60% of the variation (cross-validated error = 0.983 ± 0.269). CWM, stand-age, organic matter thickness or basal-area did not resolve these nodes further.

I observed 3 species which were significantly associated with MRT node formed by the stem exclusion and understory reinitiation stands (Table 1.2): *Platynus decentis* (IndVal = 0.79; p = 0.016), *Pterostichus coracinus* (IndVal = 0.66; p = 0.045) and *Pterostichus adstrictus* (0.84; $p < 0.001$). Catch-rates of the latter (*P. adstrictus*) were more than five times higher in stem exclusion/understory reinitiation stands than in old-growth (Figure 1.6; 0.038 ± 0.021 and 0.007 ± 0.003 specimens /trap days; T-test on transformed catch-rates: t = 4.6713, df = 6.336, p = 0.003). No species were indicators of the old-growth stands (Table 1.2).

1.4.3 Comparison of natural versus managed stands

Ordination of both uncut and managed stands resulted in a 2-dimensional solution (stress = 12.18470, Figure 1.7) showing no uniform effect of treatments on ground-beetle assemblages was visible (cut vs. uncut: MRPP, A = 0.0131, p = 0.172). Pair-wise MRPP between treatments (CPRS, intense and less intense partial cuts and controls) were non-significant (p-values greater than 0.70) with negatives values of *A* (worse than what is expected to get by chance). In fact, carabid assemblages had a stronger linear relation (Table 1.4) with basal area prior to cutting (Mantel r = 0.392, $p < 0.001$), age of the stand prior to cutting (Mantel r = 0.383, $p < 0.001$), organic matter thickness (Mantel r = 0.294, p = 0.004) and total CWM (Mantel r = 0.241, p = 0.031) than with actual basal area of the stands

(Mantel r = 0.208, p = 0.026). Partial cutting in the three sectors of Fénélon, Gaudet and Puiseaux, were meant to maintain or recreate old forest structures and did harbour carabid assemblages consistent with old uncut stands. However, CPRS of these sectors also showed carabid assemblages consistent with the old uncut stands of the region under study. Carabid assemblages in partial cuts in the Cramolet sector were the least similar to other stands. The 1/3 retention partial cuts at Cramolet contained the highest catch-rate of *Sphaeroderus stenostomus lecontei* Dejean of the whole study (0.006755) surpassing *Pterostichus adstrictus* (0.001689), which is ranked 5th in terms of abundance in this stand.

When both managed and unmanaged stands were included in dbMRT, age of the stand was again the most important variable (Figure 1.8). It was responsible for the only split of the regression tree (selected 888 times out of 1000) at 158.5 years that was similar to the dbMRT based on uncut stands. This tree however explained less variation (42.7% minimum cross-validated error = 0.932 ± 0.176) than the tree based on uncut stands alone but still stresses the importance of stand age over even silvicultural treatment for carabid assemblages in my study area.

While *Agonum quinquepunctatum* Motschulsky was found only in treated stands that were old-growth before cutting (partial cuts and CPRS in Fénélon, Gaudet and Puiseaux) (IndVal = 0.31, p = 0.02), *Pterostichus adstrictus* (0.76; p < 0.012), *Pterostichus coracinus* (IndVal = 0.66; p < 0.001), *Platynus decentis* (IndVal = 0.83; p < 0.001) and *Sphaeroderus stenostomus* (IndVal = 0.55; p = 0.015) were significantly associated with stem exclusion/understory reinitiation stands (Table 1.3). Whether *S. stenostomus* is a consistent indicator of younger stands is questionable for two reasons. First, most of its abundance (82 %) is concentrated in one sector, Cramolet (100 years old). Second, this species became a significant 'indicator' only when cut forests were also taken into account contrary to the others. *P. adstrictus* was less abundant in Cramolet partial cuts despite the fact these stands were only 100 years old before cut (Figure 1.5). By excluding these two stands from a regression of the transformed catch-rate of *P. adstrictus*, it is possible to see that the catch-rate of *P. adstrictus* linearly declines with stand age (Figure 1.5; residual standard error: 0.1631 on 21 df,

Multiple R^2: 0.537, Adjusted R^2: 0.515, F-statistic: 24.36 on 1 and 21 df, p-value: 0.00007. In this context, intense and less intense partial cuts at Cramolet would be more representative of 310 and 236 year old stands respectively according to the low catch-rates of *P. adtrictus* in these stands. However, it is important to remember that the overall assemblages characterising these stands are still different from those found in old-growth stands, as shown in the NMDS and dbMRT.

1.5 Discussion

Stand age was the most important factor determining carabid assemblages stressing that conditions prior to cutting prevailed even over silvicultural treatment in cut stands. In this context, CPRS and partial cutting had little effect on carabid composition, especially in stands that were old-growth prior to cutting (Fénélon, Gaudet and Puiseaux). This is particularly surprising in the case of CPRS, where basal area was reduced below any amount seen in uncut forests of this stage in order to emulate regenerating stands. Thus, I can say that the levels of retention used in this cohort model are not maintaining communities as it is anticipated.

Instead, applying CPRS in old-growth stands seems to maintain important attributes of old-growth stands for carabids, namely the organic layer. In black-spruce stands of the Clay belt, the bryophyte community, which is omnipresent, forms an organic layer that thickens with time since fire to modify the conditions at the ground level (chemical, physical and biological components of the soil). Such edaphic factors are influent on carabids (Lindroth, 1969a). Thus, sustaining moss layers following harvesting may explain the similarity in carabid assemblages between uncut and cut old-growth stands as these stands are already paludified and have a thick organic layer. CPRS and partial cutting practiced in old-growth stands result in more "opened" stands that have reduced basal area but still have the thick organic layer present from the preceding years of stand development (Simard *et al.*, 2008). Moreover, CPRS and partial cutting, like low severity fires, are likely to encourage paludification on the Clay belt (Lavoie *et*

al., 2005a, 2005b). *Agonum quinquepunctatum*, which was limited to harvested old-growth stands in my study, was the only obvious species which may demonstrate a shift towards more paludified stands, as this species is associated with moist, boggy areas (Larochelle and Larivière, 2003; Lindroth, 1966). In recently burned stands, Paquin (2008) has observed a similar response to increasingly open canopy by *A quinquepunctatum*.

The importance of edaphic factors may also explain why Cramolet is the only sector where an effect of cutting on carabid assemblages was perceptible. As Cramolet was the only sector that was not old-growth prior to cutting, partial cutting in this sector may have induced larger changes for carabids than cutting in old-growth, more opened and paludified stands. At 100 years old prior to harvest, Cramolet stands were only at the beginning of the canopy breakup that precedes a gradual drop in basal area and productivity. Others have shown that canopy opening through partial cutting can recreate a bryophyte community consistent with older forest types (Fenton and Bergeron, 2007). This likely occurred in the relatively young stands of Cramolet and may have had subsequent effects for carabids and the edaphic factors with which they rely. Low catch-rates of *P. adstrictus* in partial cuts at Cramolet could be indicative of a switch towards these older stand attributes, since this species was less frequent in these stands as well as in the older uncut forests. It is likely that these attributes are related to edaphic factors, since catch-rates of *P. adstrictus* were declining with stand age and the concomitant increase in paludification. This would reflect the preference of *P. adstrictus* for rather dry to moderately moist soils (Lindroth, 1966; Pearce et al., 2003) and suggests that this organism may be affected by the rising water tables or the increase in organic matter promoted by canopy opening through harvesting and trough prolonged absence of fire (Fenton *et al.* 2005; Lavoie *et al.*, 2005a; 2005b). Moreover, Paquin (2008) reported that *P. adstrictus* was most abundant in recently burned sites. In Fennoscandia, Martikainen *et al.* (2006) suggest that the affinity of *P. adstrictus* for fire could be attributed to the presence of dead wood in burned stands, but the fact that fire reduces the organic layer of the soil (Simard, 2008) could also be a plausible explanation. Moreover, control and

CPRS at Cramolet seemed more favourable for *P. adstrictus*, presumably because only the original and thinner organic layer of 100 years is present in control stand while in CPRS, stand has been scarified in 2008, seeing its organic layer be mixed with the mineral soil. However, scarification can have a negative effect on the abundance of this species in the short term (Klimaszewski *et al.*, 2005), but it may less negative than paludification in the long term.

While continued monitoring will be required to assess longer-term "recovery" following harvesting, my study of carabid assemblages 0-5 years post harvest is likely sufficient to capture the initial response to CPRS and partial cutting. Carabid studies conducted across the boreal mixedwood including western Québec (O'Connor *et al.*, non publié) and the rest of Canada (Work *et al.*, 2010) have been capable of detecting early changes in carabid assemblages in response to harvesting with similar levels of replication and sampling intensity.

However, we do expect treatment effects and the slow process of paludification to become more apparent in the coming years, particularly in the youngest sector (Cramolet) where partial cutting may have pushed these stands towards stands with structure consistent with later successional stages. Moreover, the period between beetle sampling and tree harvesting in Cramolet was shorter than in other sectors; Cramolet sites were cut in 2007 and sampled the same year and the year after, whereas the other RECPA sectors were sampled 3-5 years after logging. This may have limited the time required for carabids in Cramolet to respond to habitat changes resulting from logging. Others have shown that carabids can take several years to show a response to harvesting because even some closed forest species present before cut can maintain declining populations for several years before disappearing (Niemelä, 1993).

In my study, no species of carabids were associated to old-growth stands. This could explain in part why no distinct effect of cutting existed in these stands, since harvesting effects are often limited to old-growth specialists (Niemelä, 1993). Paquin (2008) found two species of Carabids associated with the old-growth stands of this region: *Dromius piceus* Dejean, and *Platynus mannerheimii*. *D. piceus* was absent from our study, despite seemingly adequate sampling effort

and typical catch-rate of other studies conducted in the same region (Paquin, 2008) and in boreal coniferous forests (Niemelä, 1993). However, *D. piceus* is a macropterous species associated to dead wood and tree bark with good flight abilities (Larochelle and Larivière, 2003; Lindroth, 1969; Mahar *et al.*, 1983; Martikainen and Kouki, 2003). Thus, the fact that I only used pitfall traps actually explains why I did not observe this species, as Paquin (2008) caught 12 of the 13 inviduals of *Dromius piceus* in flight-interception traps and 1 via Berlese extraction (Pierre Paquin, pers. comm.). While I did observe *Platynus mannerheimi*, it was more widely distributed among stand ages and silvicultural treatments. Paquin (2008) also found this species in stands from 70 to 97 years old, what is also consistent with my findings. Thus, to the light of my results, *Platynus mannerheimi* should not be considered an old-growth specialist.

My study does confirm previously reported trends in individual species. *Pterostichus punctatissimus* is known as a generalist in the black-spruce feather-moss domain (Paquin, 2008) and a coniferous specialist (Lindroth, 1966; Pearce *et al.*, 2003) and was found in all stand ages and cutting types. *Pterostichus adstrictus*, *Platynus decentis* and *Pterostichus coracinus* reflected moderate affinity for moist habitats (Larochelle et Larivière, 2003) and are associated with mid-successional stage in our study area and in other parts of the boreal forest (Paquin, 2008; Spence *et al.*, 1996; Work *et al.* 2004). However, Cychrini carabids, which are known mollusc specialists, (*Scaphinotus bilobus*, *Sphaeroderus nitidicolis brevoorti* Leconte, and *Sphaeroderus stenostomus*) did not show any particular trend as a group contrary to Paquin (2008). He suggested that this tribe would be particularly favoured by mid-successional stands because closed canopy would protect slugs and snails against intense sun exposure and dry conditions. In my study, *S. bilobus* (253 specimens caught vs. 180 for Paquin, 2008) was ubiquitous both in uncut forests as well as in cut stands, including CPRS. This confirms that *S. bilobus* has affinity for wet and moist soils covered with moss or litter (Larochelle et Larivière, 2003), but not necessarily "forested" sites as Paquin (2008) suggests. For the other two Cychrini species, it is difficult to draw any conclusion on habitat preference because of their low abundance in

my study (n = 37, exactly like Paquin, 2008), with the exception of *S. stenostomus* that was inexplicably more abundant at Cramolet, especially in partial cuts.

Differences in carabid composition observed between old-growth and younger mature stands is also reported by Paquin (2008) and corresponds to Harper *et al.* (2005)'s classification of old-growth structural development (>164 y). Harper *et al.* (2005) attributed this change in structural stage mainly to deadwood, as basal area of snags and log volume stop to increase around 164 years after fire. However, volumes of CWM overall and of diverse decay classes failed to explain patterns in carabid assemblages among uncut stands, but did so when harvested stands were taken into account. Deadwood is an important habitat component for carabids (Larochelle et Larivière, 2003, Lindroth, 1969a) and my results suggest that CWM may be buffering effects of silvicultural treatments on carabids in harvested stands. This does not necessarily means that CWM is not ecologically important for carabids in uncut stands, but that it might be negligible from a statistical point of view, because deadwood is also affected by the prevailing variable "age of the stand". Thus stand age would reflect primary edaphic factors affecting carabids but also deadwood components. For example, on the long term (200 years), trees and individual pieces of dead wood with large diameters become less abundant because of the decrease in basal area and productivity that occurs when stands reach c.100 years because of tree mortality and paludification (Fenton *et al.* 2005; Harper *et al.*, 2003, 2005; Lecomte, 2005). This thus could limit access to a diverse range of deadwood types for carabids. Also, the fact that CWM can be buried under the growing moss could add to his trend and modify decomposition rates and stages under the moss.

Mosses on the sites are omnipresent, and bryophyte composition and the organic layer thickness changes with forest succession (Fenton and Bergeron, 2006). However, these changes do not seem to create conditions for so called 'old growth' carabid species. This would support the hypothesis of Drapeau *et al.* (2003) that more closed and complex stands of mid-succession on the Clay belt would contain higher species diversity because paludification ultimately leads to the simplification of the stand structure. Thus lack of structural complexity and of

unique conditions could explain a lack of old-growth specialists. Absence of real compositional switch in trees and associated litter during stand development can also explain in large part the lack of carabid species associated with old-growth forests (Paquin and Coderre, 1997; Pearce *et al.*, 2003). Different litter types affect conditions at the ground-level in different ways and influence the diversity of sites potentially viable for oviposition, larval development, food supply (prey habitat) and sheltering which in turn affect carabid abundance and diversity.

1.6 Conclusion

It is not possible to affirm that the partial cuts or CPRS that we investigated on the Clay belt have pushed stands to another developmental stage according to their carabid communities. However, my findings show that simplistic inferences based solely on basal area are not sufficient for a 'viable' coarse filter approach mimicking natural dynamics. Our study supports, from a biodiversity point of view, the idea that silvicultural prescriptions of practices on the Clay belt should consider age of the stands prior to cutting as a primary factor driving carabid communities and adjust accordingly. To us, changes in the carabid fauna are attributable to the accumulation of organic matter related to stand development without fire. Younger stands, because they are less paludified, should be prioritised if our goal is to use partial cutting to advance stands to an older successional stage for biodiversity and this agrees with management recommendations made by Bergeron *et al.* (2007) for stands prone to paludification. Moreover, Harper's model (2005) considering principally live wood and standing and downed dead wood would benefit from the inclusion of moss thickness as variable determining developmental stage of black-spruce stands on the Clay belt. This also reinforces the idea that foresters in the boreal forests must adapt silvicultural practices to deal with the regional characteristics they encounter instead of employing a generalized application throughout the whole boreal forest (Gauthier *et al.* 2008b, Niemelä, 1997). Future attempts to develop alternative harvesting methods like partial cutting in younger stands could show interesting results and continued monitoring will be required to assess

longer-term "recovery" following harvest. However, the use of carabids to draw conservation guidelines for other taxa is limited (Martikainen *et al.*, 2006) and it is valuable to make the same kind of study with other organisms.

Table 1.1 Description of stands used in study. Age = time elapsed since the last stand replacing fire; TSD = time elapsed since the last disturbance; OM = organic matter thickness; BA = basal area post-treatment; BA b4 cut = basal area pre-treatment; CWM = downed coarse woody material; DK-1 to 5 and total = Decay classes, from 1 to 5 and overall.

Site	Project	Status	Age	TSD	OM	BA	BA b4 cut	Retention	Volume of CWD ($m^3 \cdot ha^{-1}$)					
			(years)	(years)	(cm)	($m^2 \cdot ha^{-1}$)	($m^2 \cdot ha^{-1}$)	(%)	DK-1	DK-2	DK-3	DK-4	DK-5	Total
Ch75	Chono	Uncut	133	133	22	27.56	27.56	100	2.68	2.89	3.11	0.00	0.00	8.68
L22	Chono	Uncut	277	277	51	22.07	22.07	100	3.16	23.85	17.97	21.21	0.00	66.21
N18	Chono	Uncut	134	134	34	31.39	31.39	100	0.00	0.00	7.40	3.61	0.00	11.02
N23	Chono	Uncut	94	94	17	45.04	45.04	100	0.00	3.67	11.10	10.29	1.86	26.93
N50	Chono	Uncut	228	228	50	20.16	20.16	100	14.18	8.52	30.80	7.82	0.00	61.33
N6	Chono	Uncut	288	288	64	21.5	21.5	100	0.00	16.73	20.97	0.95	0.00	38.66
N8	Chono	Uncut	134	134	30	34.08	34.08	100	0.00	9.53	8.36	4.18	0.00	22.08
POP	Chono	Uncut	185	185	NA	18.72	18.72	100	10.69	13.61	21.79	26.69	5.53	78.33
S1	Chono	Uncut	95	95	20	43.49	43.49	100	0.00	2.65	1.69	3.09	0.00	7.44
Cramolet Lighter PC	RECPA	Cut	100	1	26	20.45	28.12	73	7.03	4.46	33.86	22.81	0.00	68.16
Cramolet Intense PC	RECPA	Cut	100	1	26	16.57	32.17	51	14.90	7.30	14.21	14.45	0.00	50.86
Cramolet CPRS	RECPA	Cut	100	1	21	0.00	27.50	0	0.00	37.89	24.26	16.34	7.93	86.43
Cramolet Ctrl	RECPA	Uncut	100	100	23	25.24	25.24	100	27.44	14.34	56.11	32.51	1.51	131.91
Fenelon Lighter PC	RECPA	Cut	183	5	34	3.20	20.45	16	0.62	14.46	19.99	7.43	0.53	43.03
Fenelon Intense PC	RECPA	Cut	183	5	26	0.45	27.96	2	0.00	7.61	4.21	0.00	0.00	11.82
Fenelon CPRS	RECPA	Cut	233	5	36	1.34	21.55	6	0.74	34.75	23.04	2.82	8.42	69.77
Fenelon Ctrl	RECPA	Uncut	183	183	36	26.10	26.10	100	NA	NA	NA	NA	NA	NA
Gaudet Lighter PC	RECPA	Cut	233	4	39	3.75	12.22	31	0.00	11.71	20.85	12.39	0.00	44.96
Gaudet Intense PC	RECPA	Cut	233	4	44	2.20	16.37	13	1.48	49.13	28.69	35.19	11.20	125.69
Gaudet CPRS	RECPA	Cut	233	4	37	0.00	12.27	0	0.00	9.35	29.89	32.13	0.00	71.37
Gaudet Ctrl	RECPA	Uncut	233	283	49	18.95	18.95	100	0.00	2.31	12.85	0.00	19.15	34.32
Puiseaux Lighter PC	RECPA	Cut	183	5	40	7.24	15.96	45	0.00	9.69	4.04	13.55	4.63	31.91
Puiseaux Intense PC	RECPA	Cut	183	5	40	5.29	16.99	31	0.00	20.38	2.49	2.72	0.00	25.59
Puiseaux CPRS	RECPA	Cut	183	5	36	1.04	24.55	4	0.00	3.42	11.05	3.48	0.00	17.94
Puiseaux Ctrl	RECPA	Uncut	183	183	56	13.32	13.32	100	0.00	2.80	3.34	6.67	1.49	14.29

Table 1.2 Indicator species analysis for individual species associated with groupings defined by dbMRT for uncut stands (Chronosequence + control). Class 1: < 158.5 years old; Class 2: > 158.5 years old; IndVal: indicator value (species with significant indicator values (Ind. val. > 0.40 with P < 0.05) are in boldface character); P: probability value. The thick line separates species with probability value P < 0.05 (bottom) from those that are ≥ 0.05 (up).

Species	Class	IndVal	Probability
Scaphinotus bilobus	1	0.53	0.84615385
Trechus crassiscapus	2	0.40	0.53946054
Agonum gratiosum	1	0.31	0.46553447
Pterostichus stantonensis	1	0.17	0.41358641
Synuchus impunctatus	1	0.17	0.40559441
Pterostichus punctatissimus	1	0.57	0.34565435
Sphaeroderus stenostomus	1	0.29	0.20579421
Platynus mannerheimi	2	0.29	0.15184815
Pterostichus coracinus	**1**	**0.66**	**0.04495505**
Platynus decentis	**1**	**0.79**	**0.01598402**
Bradycellus lugubris	1	0.17	0.000999
Calathus ingratus	1	0.17	0.000999
Pterostichus adstrictus	**1**	**0.84**	**0.000999**
Pterostichus pensylvanicus	2	0.17	0.000999
Sphaeroderus nitidicollis	1	0.33	0.000999

Table 1.3 Indicator species analysis for individual species associated with groupings defined by MRT for all stands. Class 1: 94-158.5 years old; Class 2: 158.5-288 years old; Ind. val.: indicator value (species with significant indicator values (> 0.40 with $P < 0.05$) are in boldface character); P: probability value. The thick line separates species with probability value $P < 0.05$ (bottom) from those that are ≥ 0.05 (up).

Species	Class	Ind. val.	P
Cymindis cribricollis	2	0.06	1
Trechus crassiscapus	2	0.26	0.8991009
Harpalus herbivagus	1	0.08	0.82717283
Bradycellus neglectus	1	0.07	0.76823177
Amara erratica	1	0.07	0.76523477
Pterostichus punctatissimus	1	0.54	0.57942058
Scaphinotus bilobus	2	0.56	0.53846154
Pterostichus pensylvanicus	1	0.16	0.46653347
Lebia pumila	1	0.11	0.36363636
Bradycellus lugubris	1	0.11	0.32767233
Tachyta angulata	2	0.06	0.30569431
Platynus mannerheimi	1	0.28	0.2997003
Agonum gratiosum	1	0.48	0.14585415
Bradycellus nigrinus	2	0.12	0.10589411
Sphaeroderus nitidicollis	1	0.22	0.0949051
Agonum quinquepunctatum	2	0.31	0.01998002
Sphaeroderus stenostomus	**1**	**0.51**	**0.01498502**
Pterostichus adstrictus	**1**	**0.76**	**0.01198801**
Agonum mutatum	1	0.11	0.000999
Calathus ingratus	1	0.11	0.000999
Chlaenius sericeus	1	0.11	0.000999
Harpalus nigritarsis	1	0.11	0.000999
Platynus decentis	**1**	**0.83**	**0.000999**
Pterostichus coracinus	**1**	**0.66**	**0.000999**
Pterostichus luctuosus	1	0.22	0.000999
Pterostichus stantonensis	1	0.11	0.000999
Synuchus impunctatus	1	0.11	0.000999

Table 1.4 Mantel test results (r = Mantel statistic based on Pearson's product-moment correlation) for change in carabid assemblages related to changes in stand descriptive variables. CWM = downed coarse woody material

Stand variables	Uncut stands r	All stands (cut and uncut) r
Actual basal area ($m^2 \cdot ha^{-1}$)	0.4649***	0.2076*
Time since the last fire (or TSF, years)	0.3731*	0.3833***
Organic matter [§] (cm)	0.4790***	0.2940**
Volume of CWM[£] ($m^3 \cdot ha^{-1}$) Total	0.1734	0.2408*
Decay class 1	0.1504	0.0847
Decay class 2	-0.0534	0.1408
Decay class 3	0.1858	0.1750°
Decay class 4	0.0373	0.1667°
Decay class 5	-0.1461	-0.0488
Basal area ($m^2 \cdot ha^{-1}$) prior to cutting	(same as actual)	0.3922***
Time since last disturbance (years)	(same as TSF)	-0.0546
Retention (%)	(impossible, all 100%)	0.0268

[§] analyses with O.M. do not include POP

[£] analyses with CWM do not include Fénélon Control

° $p < 0.10$

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

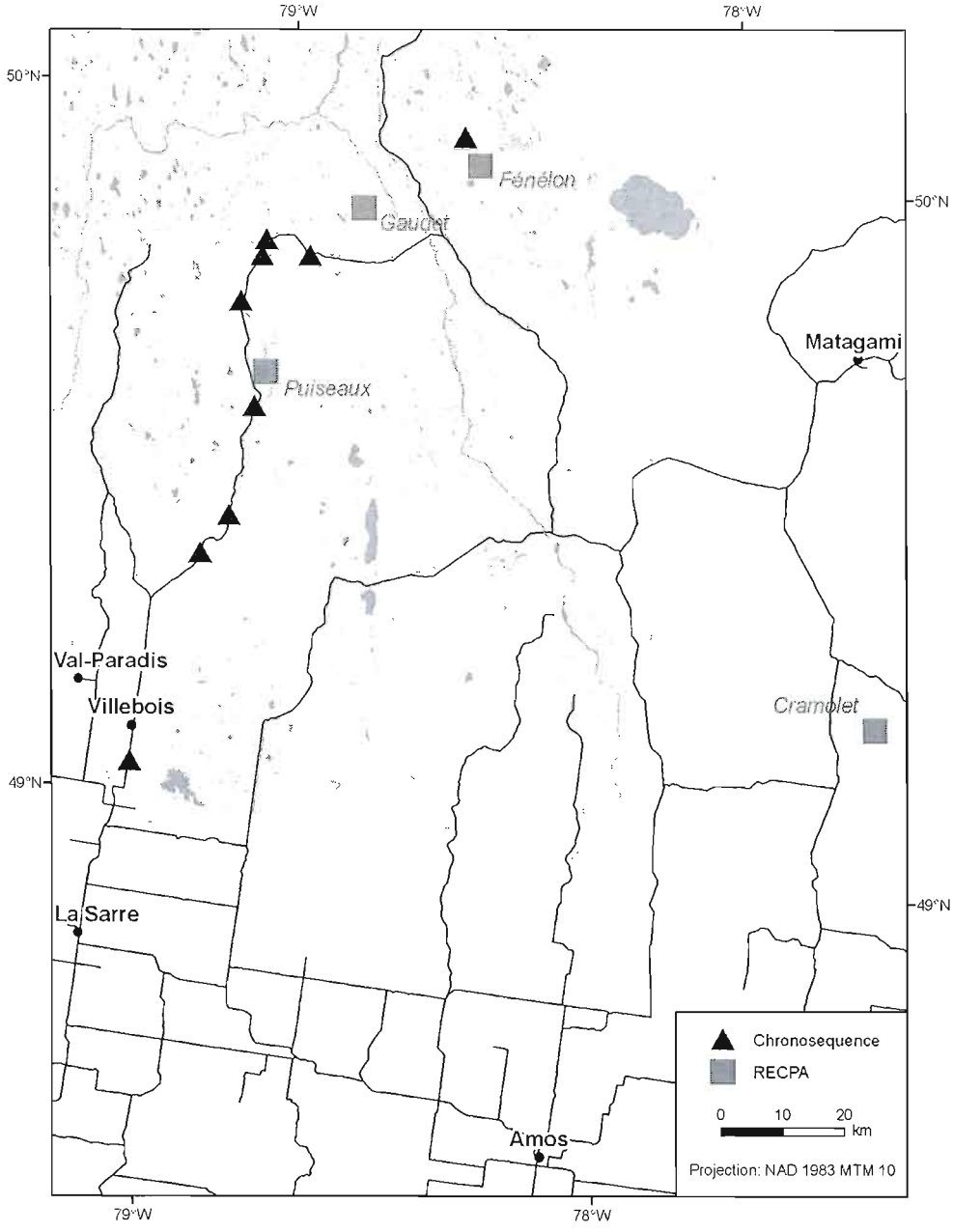

Figure 1.1 Map of the study area.

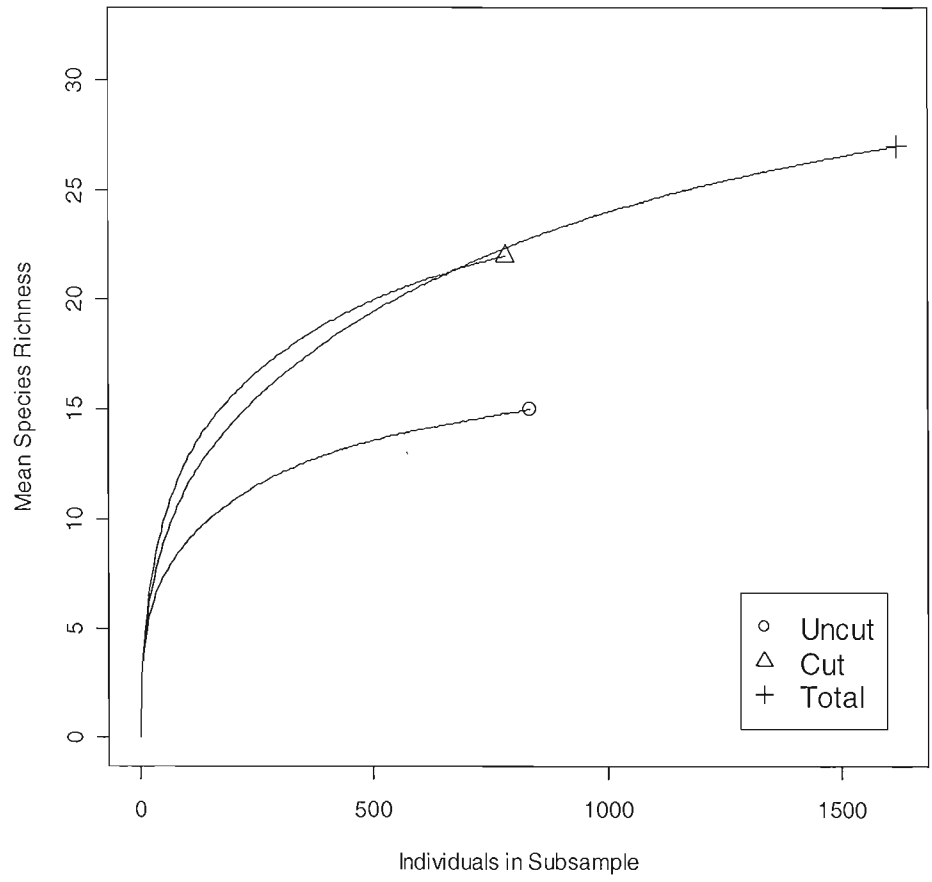

Figure 1.2 Individual based rarefaction curves using carabids for uncut stands, cut stands and all stands combined.

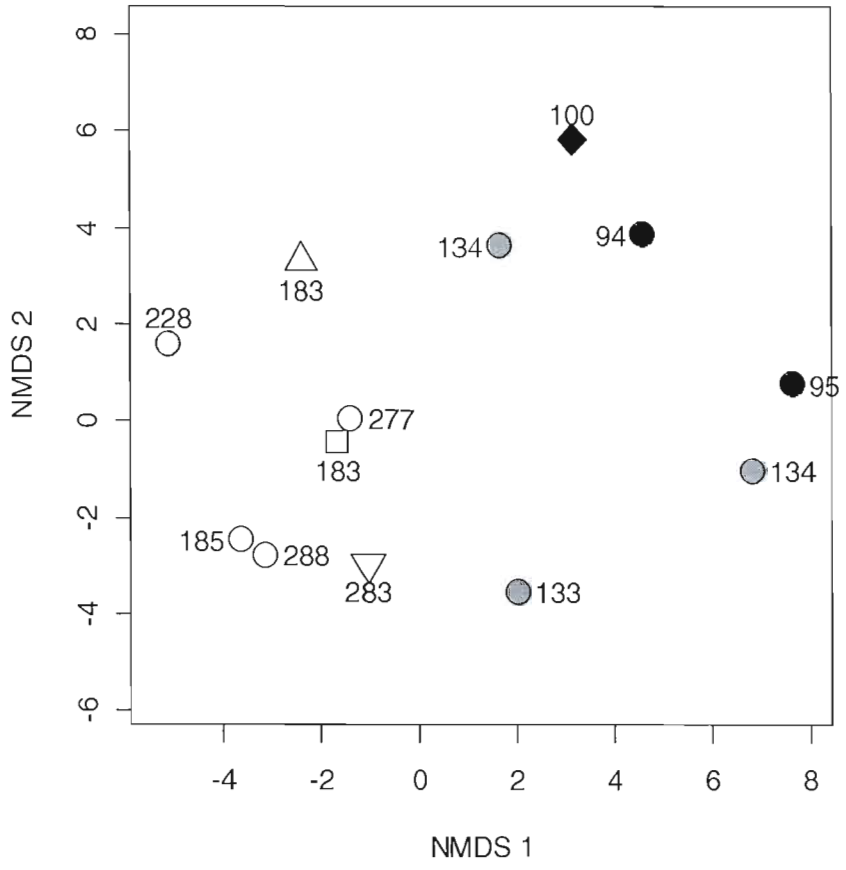

Figure 1.3 NMDS of uncut stands based on carabid assemblages (836 specimens). Circles represent the Chronosequence stands and polygons represent control stands of each sector of the RECPA (diamond = Cramolet; triangle point up = Fénélon; triangle point down = Gaudet; squares = Puiseaux). White = old-growth (O-G); gray = understory reinitation (UR); black = stem exclusion (SE). O-G vs. UR: MRPP, A = 0.127, p = 0.0168; O-G vs. SE: MRPP, A = 0.2944, p = 0.0088; SE vs. UR: MRPP, A: 0.01133, p = 0.305; O-G vs. SE + UR: MRPP, A = 0.2252, p < 0.0002.

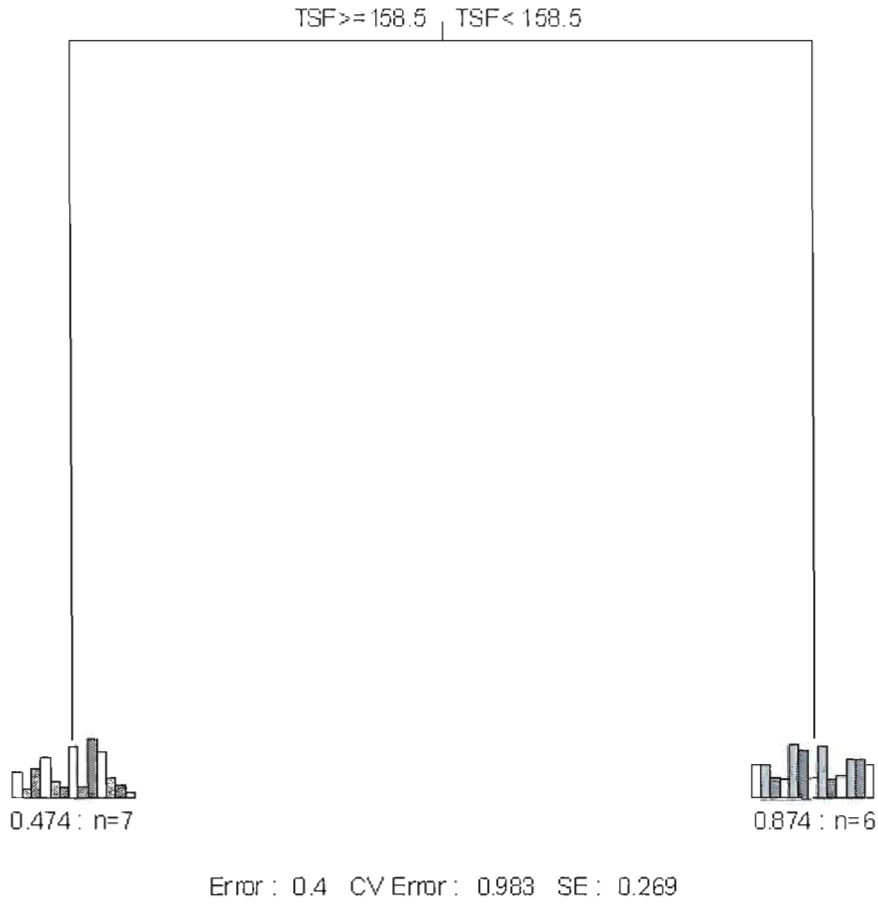

Figure 1.4 dbMRT of uncut stands based on carabid assemblages resgressed against stand age (TSF) and structural variables (see text for more details).

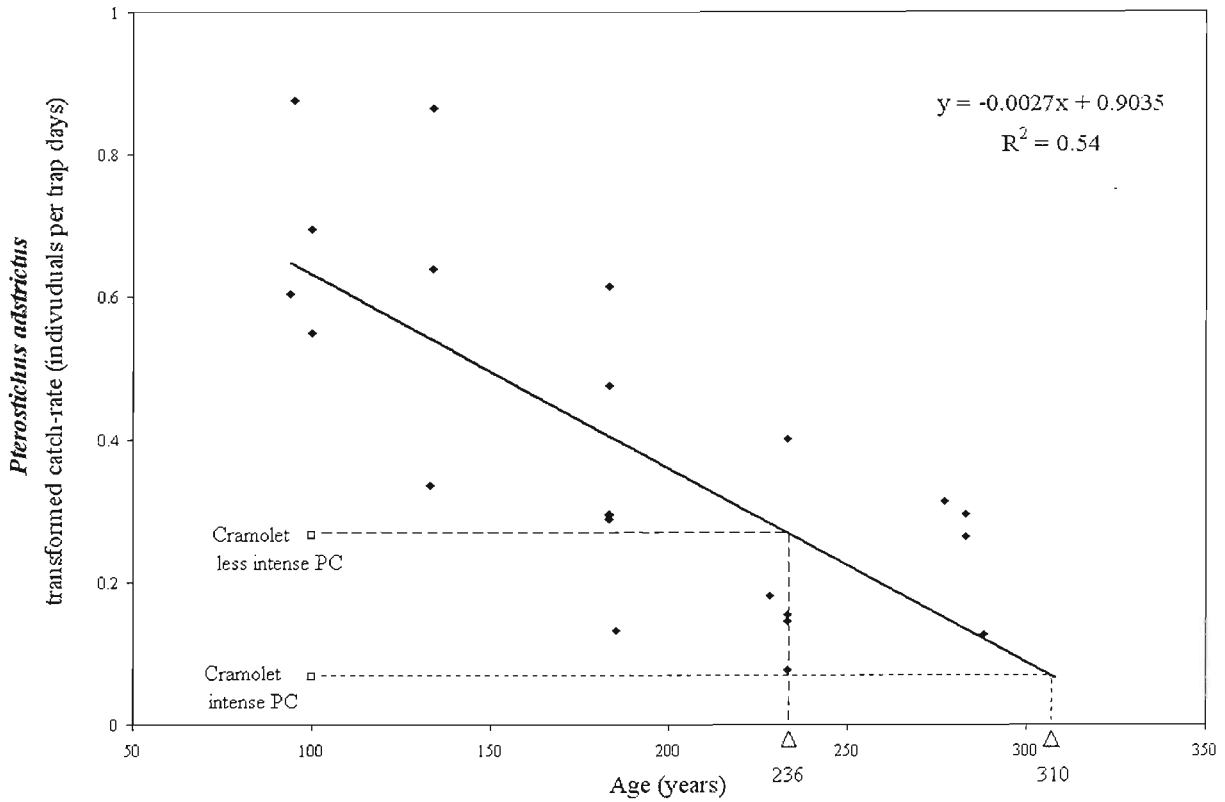

Figure 1.5 Relation between catch rates of *P. adstrictus* (transformed) and stand age for all study stands (cut and uncut) excluding partial cuts in Cramolet (white squares). Equations and multiple R^2 are presented on the graphs. Dashed lines lead to the emulated age of partial cut stands in Cramolet according to their catch-rates of *P. adstrictus*, calculated using the equation shown.

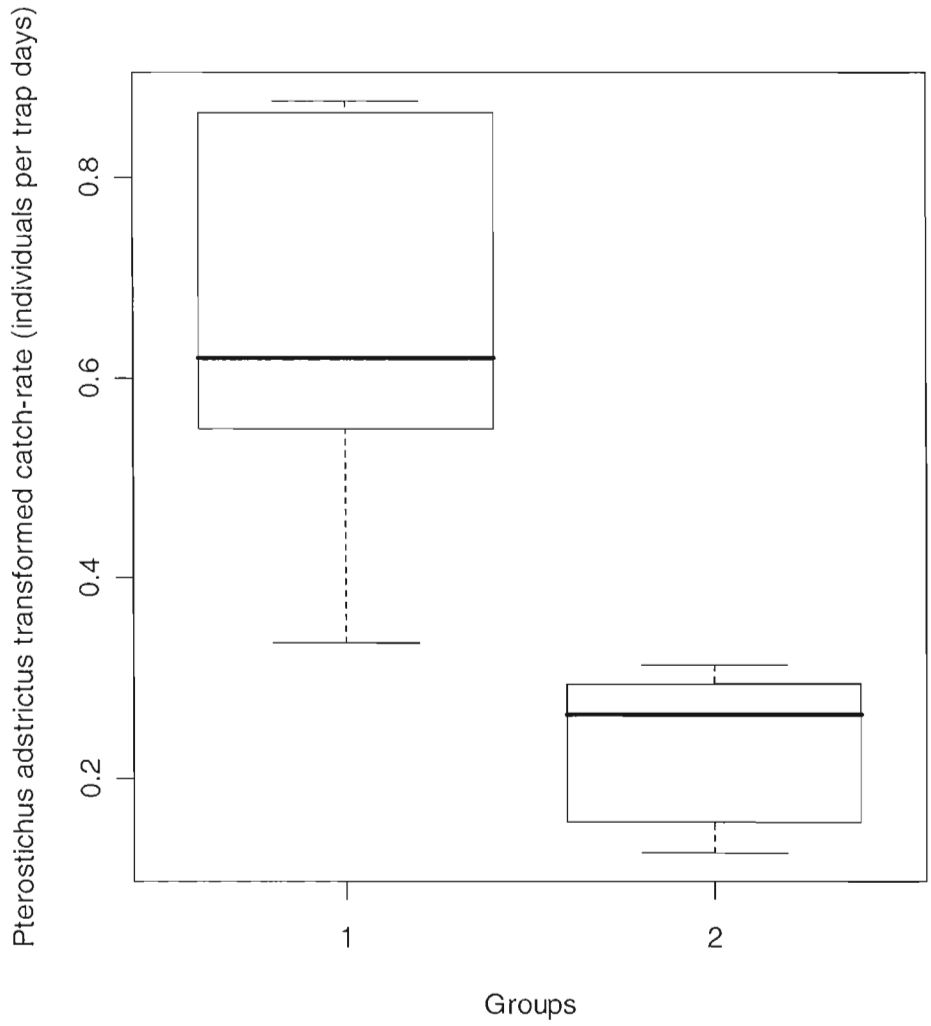

Figure 1.6 Difference in the catch-rate of *P. adstrictus* in two groups of uncut stands (understory reinitiation and stem exclusion stages vs. old-growth stands). T-test on transformed catch-rates: t = 4.6713, df = 6.336, p = 0.003.

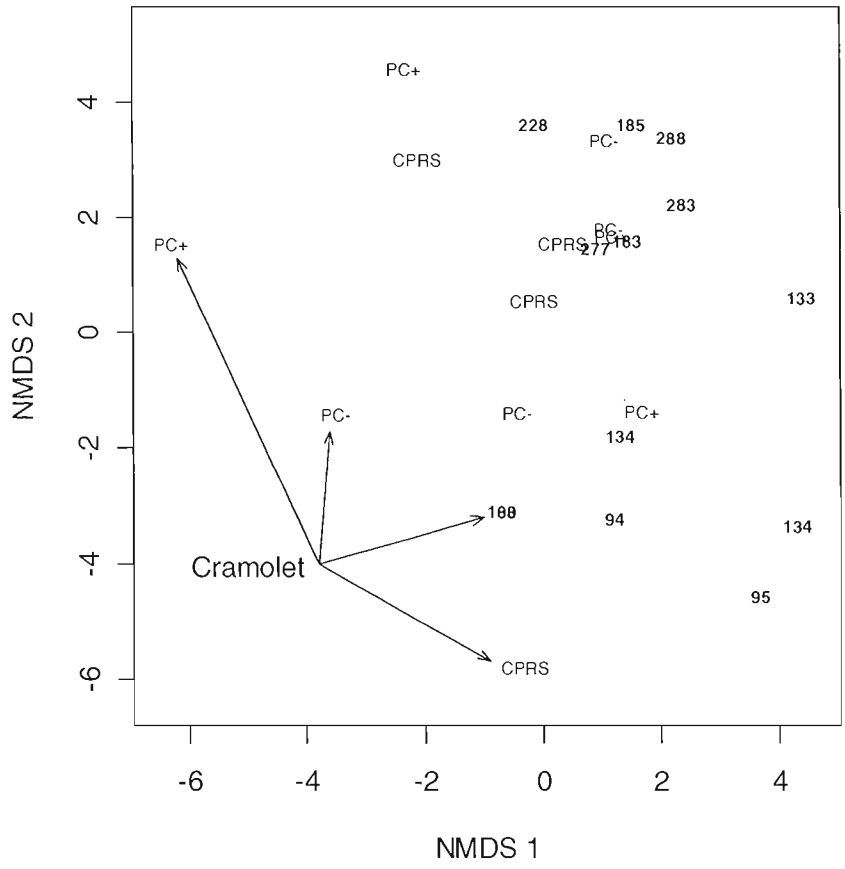

Figure 1.7 NMDS (stress = 12.19) of uncut and treated stands based on carabid assemblages (1 618 specimens). Uncut stands are represented by numbers (their age) and cut sites by the acronym of their treatment (PC+: intense partial cut, PC-: less intense partial cut, CPRS: logging with protection of advance regeneration and soils). Cut vs. uncut: MRPP, $A = 0.0131$, $p = 0.172$. Note: **arrows** are used only to identify stands in Cramolet and are **not vectors** in the ordination.

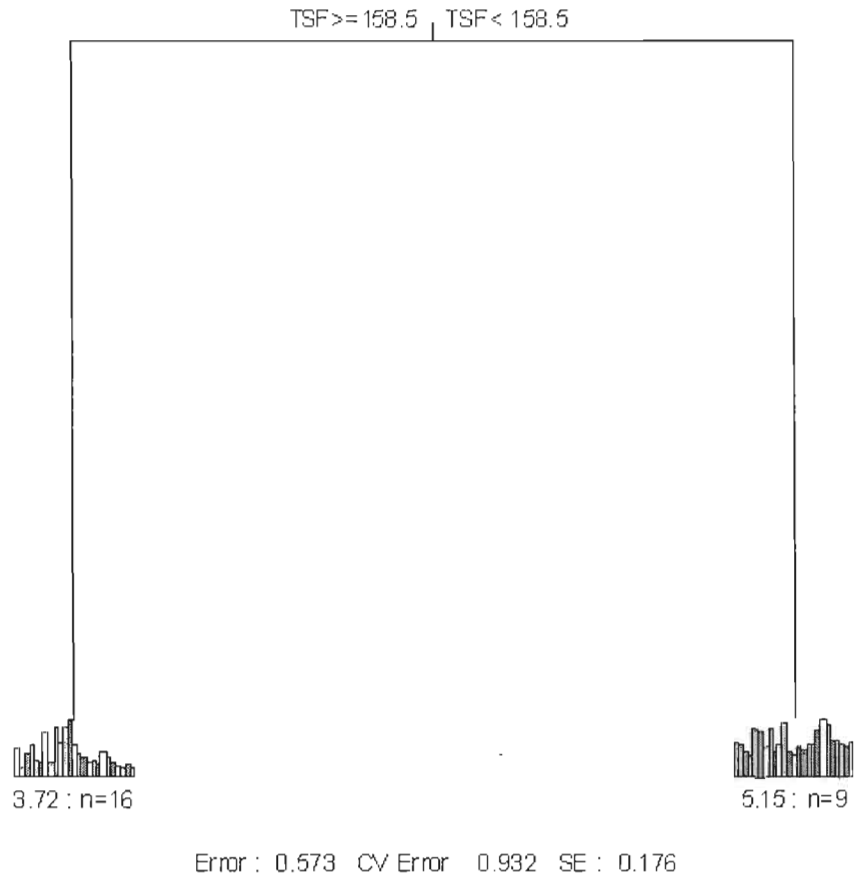

Figure 1.8 dbMRT of all stands (cut and uncut) based on carabid assemblages resgressed against age (TSF) and structural variables (see text for more details).

1.7 Annex

Table 1.5 Abundance of carabids in each stand.
(four letter abbreviations and complete names with scientific authorities precede)

Agon grat = *Agonum gratiosum* (Mannerheim); Agon muta = *Agonum mutatum* (Gemminger & Harold); Agon quin = *Agonum quinquepunctatum* Motschulsky,; Amar erra = *Amara erratica* (Duftschmid); Brad lugu = *Bradycellus lugubris* (LeConte); Brad negl = *Bradycellus neglectus* (LeConte); Brad nigr = *Bradycellus nigrinus* (Dejean); Cala ingr = *Calathus ingratus* Dejean; Chla seri = *Chlaenius sericeus sericeus* (Forster); Cymi crib = *Cymindis cribricollis* Dejean; Harp herb = *Harpalus herbivagus* Say; Harp nigr; *Harpalus nigritarsis* C.R. Sahlberg; Lebi pumi = *Lebia pumila* Dejean; Plat dece = *Platynus decentis* (Say); Plat mann = *Platynus mannerheimi* (Dejean); Pter adst = *Pterostichus adstrictus* Eschscholtz; Pter cora = *Pterostichus coracinus* (Newman); Pter luct = *Pterostichus luctuosus* (Dejean); Pter pens = *Pterostichus pensylvanicus* LeConte; Pter punc = *Pterostichus punctatissimus* (Randall); Pter stan = *Pterostichus stantonensis* [*bryanti*] Ball; Scap bilo = *Scaphinotus bilobus* (Say); Spha niti = *Sphaeroderus nitidicollis nitidicollis* Guérin-Méneville; Spha sten = *Sphaeroderus stenostomus lecontei* Dejean; Synu impu = *Synuchus impunctatus* (Say, 1823); Tach angu = *Tachyta angulata* Casey; Trec cras = *Trechus crassiscapus* Lindroth.

	N23 94y	S1 95y	Ch75 133y	N18 134y	N8 134y	POP 184y	N50 228y	L22 277y	N6 288y
Agon grat	0	1	0	0	1	0	1	0	0
Agon muta	0	0	0	0	0	0	0	0	0
Agon quin	0	0	0	0	0	0	0	0	0
Amar erra	0	0	0	0	0	0	0	0	0
Brad lugu	0	0	0	0	0	0	0	0	0
Brad negl	0	0	0	0	0	0	0	0	0
Brad nigr	0	0	0	0	0	0	0	0	0
Cala ingr	0	3	0	0	0	0	0	0	0
Chla seri	0	0	0	0	0	0	0	0	0
Cymi crib	0	0	0	0	0	0	0	0	0
Harp herb	0	0	0	0	0	0	0	0	0
Harp nigr	0	0	0	0	0	0	0	0	0
Lebi pumi	0	0	0	0	0	0	0	0	0
Plat dece	2	7	6	1	6	0	0	2	0
Plat mann	0	0	0	0	0	0	0	0	0
Pter adst	35	69	10	28	70	4	5	9	2
Pter cora	15	14	0	0	4	0	0	0	0
Pter luct	0	0	0	0	0	0	0	0	0
Pter pens	0	0	0	0	0	0	0	0	0
Pter punc	13	32	28	7	30	17	10	11	12
Pter stan	0	0	1	0	0	0	0	0	0
Scap bilo	2	3	1	9	28	6	10	5	4
Spha niti	1	0	0	0	2	0	0	0	0
Spha sten	0	1	0	0	0	0	0	0	0
Synu impu	0	4	0	0	0	0	0	0	0
Tach angu	0	0	0	0	0	0	0	0	0
Trec_cras	0	1	1	0	4	0	10	0	1

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Agon grat	8	1	1	5	1	1	0	3	1	0	1	0	2	1	0	0
Agon muta	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agon quin	0	0	0	0	1	0	6	0	0	1	0	0	1	3	0	0
Amar erra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Brad lugu	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Brad negl	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Brad nigr	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Cala ingr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chla seri	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cymi crib	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Harp herb	3	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Harp nigr	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebi pumi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plat dece	13	5	4	7	0	2	0	6	0	0	0	1	6	1	3	1
Plat mann	3	3	11	0	0	0	0	2	0	0	0	1	2	0	1	0
Pter adst	70	15	3	45	29	27	53	13	8	8	4	16	20	20	19	19
Pter cora	14	14	0	24	0	0	0	1	0	0	0	0	0	0	0	0
Pter luct	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Pter pens	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Pter punc	4	6	8	9	14	8	20	8	8	26	11	35	25	29	30	32
Pter stan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scap bilo	3	4	3	12	13	27	20	14	15	12	8	6	7	11	15	15
Spha niti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spha sten	6	6	12	4	0	1	0	0	2	1	0	1	0	0	0	0
Synu impu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tach angu	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Trec_cras	1	1	0	0	0	2	2	2	0	0	2	0	0	0	0	3

CHAPITRE II

RESPONSE OF SPIDERS (ARANEAE) TO ADAPTED PARTIAL CUTTING TO EVALUATE COARSE FILTER APPROACH IN BLACK SPRUCE STANDS PRONE TO PALUDIFICATION

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Manuscrit en voie d'être soumis à Forest Ecology and Management

2.1 Abstract

In this chapter, I use epigaeic spiders (Araneae) to evaluate whether partial cutting and a cohort model of ecosystem management are sufficient to preserve biodiversity found in mature and old-growth black spruce stands of the northern Clay belt in Québec (Canada). I compared spider fauna in partial cuts, clear-cuts (CPRS) and uncut control stands to a chronosequence of mature and over-mature naturally regenerated stands (94-288 years since the last fire). In stands that were old-growth prior to cutting, harvesting had strong repercussions on spider assemblages that were not attenuated by partial cutting. The most obvious changes in spider assemblages were related to the increase of open habitat specialists and certain resident generalist species. Spider assemblages found after cutting were not consistent with those found in mature and older stands representing the natural variability present in the study area. Therefore, the current use of partial cutting will need to be modified to maintain spider assemblages and meet coarse filter goals. However, I did not observe a similar recruitment effect of these species in partial cuts with 2/3 retention in younger, more closed stands. This practice may have the potential to recreate stand conditions consistent with old-growth, but further verification over longer time periods is required. I suggest that age of the stands prior to cutting, their degree of paludification as well as remnant basal area are important factors to consider when evaluating the efficacy of partial cutting to maintain forest spider assemblages.

2.2 Introduction

In the absence of anthropogenic pressures, the proportion of old stands in boreal forests is determined by past and present natural disturbance regimes (Bergeron *et al.*, 2004; Gauthier *et al.*, 2000; Simard *et al.*, 2008). These forests tend to diversify in structure with age (Franklin *et al.*, 2002; Lähde *et al.*, 1999). Structural complexity of old stands is thought to be of primary importance for biodiversity (Boudreault *et al.*, 2002) and is a primary target in coarse-filter conservation approaches. However, many approaches to management of boreal forests tend to truncate stand age and homogenize forest structures in turn posing a risk for biodiversity (Cyr *et al.*, 2009; Drapeau *et al.*, 2003).

In regions with poorly drained soils and propitious climate, paludification can have a large effect on stand structure. Paludification is a dynamic process involving a gradual rise in the water table promoted by peat accumulation and *Sphagnum* spp. invasion (Fenton *et al.*, 2005; Lavoie *et al.*, 2005a, 2005b). As stands age, edaphic conditions become less favourable for tree growth and regeneration leading to less productive stands. Old stands thus tend to be more open than previous mature stages when they get paludified (Lavoie *et al.*, 2005a).

To preserve biodiversity across managed boreal landscapes, coarse filter approaches and natural disturbance based management have been widely proposed (Attiwill, 1994; Franklin, 1993; Galindo-Leal and Bunnel, 1995; Hunter, 1990). This approach advocates the maintenance and the creation of forest attributes (e.g. structure and composition) consistent with natural disturbance regimes at large scales. It is hoped that these habitats should preserve the vast majority of the biodiversity adapted to these conditions (Gauthier *et al.*, 2008a, 2008b; Hunter, 1990; Lemelin and Darveau, 2006).

While intuitively attractive, the effectiveness of the coarse filter approach remains largely untested scientifically (Rempel *et al.*, 2004) and requires empirical validation with a variety of taxa. Spiders (Araneae) are often chosen as ecological indicators for their sensitivity to habitat change, their diversity and abundance and for logistical reasons related to ease of collection and their

relatively well-known taxonomy (see review by Pearce and Venier (2006) and references therein). While spiders assemblages are known to differ after recent clear-cutting and wildfire (Buddle *et al.*, 2000, 2006; Larrivée *et al.*, 2005; Siira-Pietikäinen *et al.*, 2003) they start to converge within 30 years of stand recovery (Buddle *et al.*, 2000, 2006). Similar results were found after logging and prescribed burning (Huhta, 1971). While some general trends have begun to emerge, the biggest dissimilarity between these disturbances is spiders are less abundant following fire than logging (Buddle *et al.*, 2000; Huhta, 1971; Larrivée *et al.*, 2005). Species commonly associated with closed canopy or older forests that remain after clearcut are gradually replaced by open habitat species (Buddle *et al.*, 2000; Huhta, 1971; Pearce and Venier, 2004). However, response of spiders to alternative harvesting methods like partial cutting is poorly documented (Buddle and Shorthouse, 2008). In Fennoscandia, studies demonstrate that changes in spider assemblages are proportional to intensity of harvesting treatments (Matveinen-Huju and Koivula, 2008; Matveinen-Huju *et al.*, 2006; Siira-Pietikäinen *et al.*, 2003) but it is unclear how much retention must be prescribed to maintain spider assemblages consistent with mature and old-growth forests.

To preserve biodiversity and maintain a supply of commercial fibre, Bergeron *et al.* (1999) proposed a cohort-based model that includes partial cuts to maintain and recreate old stand attributes in a context of ecosystem management (see also Bergeron *et al.*, 2002 and Bouchard, 2008). To assess whether the cohort model is a viable coarse filter approach, it is necessary to characterise long-term stand development following disturbance and identify the major differences between natural and managed landscapes (Bergeron *et al.*, 2008) in terms of biodiversity.

In this chapter, I used a series of uncut stands differing in their age to characterise the natural variability of spider assemblages in my study area in relation with long-term stand development. This chronosequence serves as a natural reference for further comparison of spider assemblages of cut stands to evaluate the potential of partial cuts to emulate old stand structures. According to

the coarse filter principles, partial cuts would favour spider assemblages that are consistent with older, more structurally complex but also more opened stands.

2.3 Material and Methods

2.3.1 Study area

My research took place on the northern portion of the Abitibi Claybelt in north-western Québec (Canada) (49° 00'-50° 00'N; 77° 30'-79°0 8'W, Elevation: 256-314m) (Figure 1.1). This geophysical unit of heavy clay soils and till also extends into Ontario and covers *ca.* 125 000 km^2 (Lefort *et al.*, 2002). Topography is flat, ranging from 255 and 280 m in elevation. Daily average temperatures at La Sarre, Amos and Matagami (Figure 1.1) are respectively 0.7, 1.2 and -0.7 °C and average annual precipitations are of 889.8, 918.4 and 905.5mm (Environment Canada, 2005). These characteristics lead to paludification in this region (Lavoie *et al.*, 2005a, 2005b; Lefort *et al.*, 2002).

Study sites were all part of the black spruce-feather moss bioclimatic domain, which covers about 28% of the province of Québec and represents an economically important source of wood. Stands in this region are dominated by black spruce (*Picea mariana* Lamb.). Other tree species do occur but represent a minor component of the landscape and the most common are principally found only in early seral stages (*Pinus divaricata* (Ait.) Dumont, *Populus tremuloides* Michx.). The herb layer is dominated by ericaceous species (Fenton *et al.*, 2007). Exposed mineral soil is rare, lichens are common and bryophytes are omnipresent, with species like *Pleurozium shreberi*, *Dicranum polysetum*, *Hylocomium splendens*, *Ptilium cristacastrensis* and *Sphagnum* occupying most of the ground layer (Fenton *et al.*, 2007). In some cases, moss mats can be more than 1.5 meters thick, especially in stands originating from low severity fires (Fenton *et al.*, 2005).

2.3.2 Chronosequence

I sampled spiders from 9 stands (see Table 1.1 and Figure 2.1) within a chronosequence of stands that vary in age from the last major fire (Bergeron *et al.*, 2001; Boudreault *et al.*, 2002; Fenton *et al.*, 2005; Lecomte, 2005). Stand

structure along this time-since-fire (TSF) gradient can be characterized, according to Harper *et al.* (2005), by four major phases of development after stand-replacing fire: stand initiation (0-34 years), stem exclusion (34-96 years), understory reinitiation (96-164) and old-growth (> 164 years). Unlike mixedwood stands, black spruce stands show little compositional change in terms of tree species with TSF on the poorly drained soils of the Ontario-Québec Claybelt. Rather these stands develop structural complexity through a succession of single species cohorts of black spruce (Harper *et al.*, 2005). The two first stages are composed of a single cohort of trees that grow into a mature stand with stems of smiliar diameter and closed canopy. This relatively simple structure persists approximately 100 years until dead wood inputs increase and basal area decreases with the concurrent break-up of the canopy caused by natural tree mortality (Harper *et al.*, 2005; Lecomte *et al.*, 2006). Understory reinitiation then occurs with development of small black-spruces in the understory to generate structural complexity. However, with time without fire, a thick moss layer develops and limits rising proportions of new roots to the organic layer, thus impeding growth and establishment of the younger cohorts (Fenton *et al.*, 2005).

Age of the stands was determined using dendrochronology by Boudreault *et al.* (2002) and Fenton *et al.* (2005). However, this method can underestimate the actual time since the last fire. For example, Lecomte *et al.* (2006) estimates the oldest site (288 years old) to be over 700 years old using radiocarbon-dating. However, not all sites have been carbon-dated and stand ages based on tree-rings still provide a means to make relative comparisons and inferences regarding stand development. Basal area and organic matter thickness at the stand level were provided by Fenton et al. (2005). Downed coarse woody material (CWM) and finer-scale estimates of basal area (20m x 20m plots) were measured by J. Jacobs (*unpublished data*) in the summer of 2008. For CWM, two star plots were established in each stand (Ståhl *et al.*, 2001) consisting of three 20 m transects radiating from a common midpoint (the center of my sampling stations). For each intersected piece of CWM larger than 5 cm in diameter, exact diameter was recorded and the decomposition stage was determined using a five class system

(modified from Maser *et al.*, 1979), class 5 being the most decayed. Stand level volumes of CWM were computed using the Van Wagner formula (Van Wagner, 1968).

2.3.3 RECPA (Réseau d'expérimentation de coupes partielles de l'Abitibi)

In addition to the chronosequence sites, I sampled spiders from 4 experimental subunits (sectors) of the RECPA partial cutting network (for more generalities (mission of the RECPA, other existing sectors, industrial partners), see the same section in the previous chapter and Fenton *et al.*, 2008). Cramolet, Fénélon, Gaudet and Puiseaux were within 120 km of each other (Figure 1.1). Stands from these sectors were between 100 and 283 years old before harvest (see Table 1.1) and were allocated to 3 treatments: 1) controls (untouched stands representative of the stands before logging); 2) partial cutting with variable retention and 3) CPRS (French acronym meaning "logging with protection of advance regeneration and soils"). CPRS is the most commonly used harvesting practice on the Clay belt (Lefort *et al.*, 2002) where tree removal can be > 99% and skid trails resulting from machinery activity are limited to ≤ 25% of the forest floor to minimize impacts on small stems from harvesting machinery. An exception is in Cramolet, where scarification was applied in 2008 to mix organic with mineral soils. Permanent sampling plots were established in all treatments of each sector following the standards of the Ministère des Ressources naturelles et de la Faune (Direction des inventaires forestiers du Québec, 2006). Environmental data for the RECPA was supplied by the RECPA project (unpublished data)

2.3.4 Spider sampling

I sampled spiders during the summers of 2007 and 2008. Within each of the chronosequence stands, 2 sampling stations were installed. Within each of the 4 RECPA sectors (Cramolet, Fénélon, Gaudet and Puiseaux), 3 sampling stations were installed in association with permanent sampling plots already existing in control and CPRS stands. In partial cuts, I used a total of 6 (3 sampling stations in low retention and 3 others in high retention areas) that captured the gradient of

retention left within this treatment. In the Cramolet sector, 1/3 and 2/3 retention areas were part of the silvicultural prescription and increased the overall range of retention in my study. Each sampling station consisted of 3 pitfall traps placed in a triangle where each trap was placed 5-10 meters from the center. For more details about traps, sampling dates and specimen preservation and sorting, please refer to the equivalent section in the previous chapter.

I identified mature spider specimens to species-level using taxonomic publications developed by Pierre Paquin and Nadine Dupérré (2003, 2006). Additional references were also used when necessary (Dondale and Redner, 1978, 1982, 1990; Dupérré and Paquin, 2007; Platnick and Dondale, 1992) Nomenclature follows Platnick (2009). Sex was also determined for every specimen but will not be taken into account in the analyses.

2.3.5 Data analyses and statistical approaches

I used individual-based rarefaction curves to evaluate whether sampling was sufficient to adequately characterize species assemblages within uncut forests only, cut stands only, and both combined. Rarefaction curves were made using vegan (Oksanen *et al.*, 2006) in R version 2.4.0 (R Core Development Team, 2006). All further statistical analyses were also done using this software.

I standardized spider abundances to daily catch-rates by dividing the number of individuals summed at the stand level by the number of active trapping days. These catch-rates are used in all further analyses to allow for stand level conclusions relevant to the coarse filter approach and to forest management. These catch-rates were square-root transformed prior to every analysis.

To characterize spider response to natural stand dynamics, I used all uncut stands (Chronosequence + RECPA's control stands). According to their age, natural stands in our region are supposed to form *a priori* groupings corresponding to the structural stages proposed by Harper *et al.* (2005). The range of age of the stands that I studied fall into three different classes: stem exclusion (34-96 years), understory reinitiation (96-164 years), and old-growth (>164 years).

I used non-metric multidimensional scaling (NMDS) to characterize spider assemblages because it does not require excessive statistical assumptions that may be ecologically unsupported or unwarranted (McCune and Grace, 2002). Our ordinations were based on Bray-Curtis distance as this measure eliminates shared 'absences' or 'double zeros' which would otherwise be treated as a positive measure of assemblage similarity between sites (Legendre and Legendre, 1998) and is more sensitive to responses of rare species than Canberra-metric distance. I used "bestnmds" function in the vegan library (Oksanen *et al.*, 2006) for all ordination procedures. In these analyses, I used 40 random starting configurations each with up to 100 iterations (minimizing the risk of the iteration falling into a local minimum) to find the lowest stress solution.

To link characteristics of the stands with beetle assemblages, I used two complementary statistical methods. First, I used distance-based multivariate regression trees (dbMRT, De'ath, 2002) to group spider assemblages based on stand characteristics. Again, Bray-Curtis distances were used. To understand how spider assemblages changed with stand development, only the spider assemblages from uncut forests were included in the dbMRT under the constraints of the age of the stand (in years), thickness of organic matter (cm), total basal area ($m^2 \cdot ha^{-1}$) and volume of total coarse woody debris as well as volumes of each of its 5 decay classes ($m^3 \cdot ha^{-1}$) (see Table 1.1 for stand description). To understand the interaction between forest management and stand development, spider assemblages of both uncut and cut stands were constrained by the same covariates as the previous analysis (age of treated stands is their age before cut) while adding harvesting treatment, basal area prior to treatment ($m^2 \cdot ha^{-1}$), percentage of retention and time since the last disturbance (cut for treated stands and fire for regenerated stands) as covariates (again, refer to Table 1.1). Final tree size was chosen based on cross-validation and consensus based on 1000 trees. A cross-validated error of 0 indicates a perfect predictor and the predictive power of trees decreases as this number increases (De'ath, 2002). dbMRT were performed using the "mvpart" from the library of the same name (De'ath, 2006).

I used indicator species analyses (Dufrêne and Legendre, 1997, "duleg" function from "labdsv" Roberts, 2006) to identify species associated with each terminal node of the dbMRTs. In this type of analysis, indicator values (IndVal) are the product of the relative frequency and the relative abundance of a single species to give a measure combining species fidelity (present in all the sites of a group) and specificity (present in one group in particular) for a group of sites. Because our analyses show fewer groups than Dufrêne and Legendre (1997), I used a more conservative criterion than what they used by considering significant ($p < 0.05$) indicator values greater than 40 % as representative of strong indicator species, as done by Buddle *et al.* (2006).

I also used Mantel tests (vegan library from Oksanen *et al.*, 2006) to link stand variables with spider assemblages specifically to evaluate linearity of the changes of spider assemblages with stand variables. Like MRT, Mantel test is a non-parametric test but instead of working as constrained clustering (De'ath, 2002), it aims to test for a linear relationship between two different distance matrices of the same objects (Legendre and Legendre, 2008) (for example, between the dissimilarity of the spider assemblage between stands and the dissimilarity of each value of environmental variable characterising these stands). In our case, this is pertinent since many stand characteristics show a linear relationship with time since fire (Fenton *et al.*, 2005). The strength of relationship (r) between the matrices is the Standardized Mantel statistic (McCune and Grace, 2002). Distance measures used for this test were Bray-Curtis for spider assemblages and Euclidean for every stand variable, as double zeros in stand characteristics are meant to count for the dissimilarity between stands. Thus, MRT is more appropriate to depict break points in spider assemblages like the different successionnal stages from Harper's model (2005) but would be less efficient to show gradual changes in the spider assemblages associated to gradual changes in their environment. In our case, both are interesting and thus both methods will be used.

2.4 Results

2.4.1 General

I caught 11 628 adult specimens of spiders over 37 889 trap days (2006-2007). Cut stands harbored more individuals and had higher catch rates (7890 individuals and 0.3571 spiders/day) than uncut stands (3648 individuals and 0.2347 spiders/day). These differences reflect in part increased sampling effort in partial cut stands (22 345 and 15 544 trap-days respectively). Overall, I observed 136 species in 85 genera and 15 families (see Annex and Figure 2.2). Thirty-four species were found only in harvested stands compared to 15 species found only in uncut forests. Thirty-nine species were double- or singletons (See Annex). I included these rare species in the analyses because removing them did not have any significant changes on the outcoming conclusions.

Linyphiidae was the most diverse family represented by 71 different species. However, 8 of the 11 most abundant species were Lycosidae (*Pardosa moesta* Banks, *Pardosa hyperborea* (Thorell), *Trochosa terricola* Thorell, *Pardosa uintana* Gertsch, *Pirata cantralli* Wallace & Exline, *Pardosa mackenziana* (Keyserling), *Pardosa xerampelina* (Keyserling) and *Alopecosa aculeata* (Clerck) and represented almost half (48,23%) of all adult specimens collected. Other dominant species included *Gnaphosa microps* L. Koch (Gnaphosidae), *Cybaeopsis euopla* (Bishop & Crosby) (Amaurobiidae) and *Hahnia cinerea* Emerton, 1890 (Hahniidae) which respectively ranked 3rd, 8th and 10th overall. Four of the next 6 most abundant species were Linyphiidae (*Sciastes truncatus* (Emerton), *Diplocentria bidentata* (Emerton), *Pocadicnemis americana* Millidge and *Agyneta olivacea* (Emerton), the others being a Lycosidae (*Pirata bryantae* Kurata, 15th overall) and a Liocranidae (*Agroeca ornata* Banks, 16th overall). Altogether, these 17 species accounted for almost 79.68% of total catches.

2.4.2 Changes in spider assemblages with natural stand development

Spider assemblages in uncut stands within the chronosequence were described using a two dimensional NMDS ordination (Figure 2.3, stress =11.20), with axis 1

corresponding with stand development. This unconstrained ordination also showed spider assemblages from understory reinitiation stands to be more similar to old-growth stands. Similar results were obtained using the dbMRT where stand age and structural variables were considered simultaneously. In this analysis stand age was always selected as the most meaningful factor explaining spider composition (Figure 2.4). Spider assemblages in stem-exclusion stands (age < 116.5) were initially separated from older stands (age ≥ 116.5), which were further divided into old-growth and understory reinitiation stages again according to their age (≥ 158.5 or age < 158.5 respectively). This corresponds to Harper's model (2005) of stand development. This 3-leave regression tree explained 43% of the variance and was well supported by cross validations as it was picked 993/1000 times but did have a relatively high cross-validated error (0.993 ± 0.136). Additional environmental variables including basal area and coarse woody material did not resolve theses nodes further. However, changes in spider assemblages showed the strongest linear relationship with changes in basal area (Mantel test: $r = 0.567$, $p < 0.001$). However stand age (Mantel $r = 0.374$, $p = 0.004$) and organic matter thickness (Mantel $r = 0.451$ $p = 0.003$) were also linearly related with spider assemblages. These three variables are closely related (Fenton *et al.*, 2005) and it is thus not suprising to see them influencing spider assemblages in similar ways.

Within the uncut stands, 3 species showed strong affinities with the stem-exclusion stage (*Pirata montanus* Emerton, *Lepthyphantes alpinus* (Emerton) and *Walckenaeria exigua* Millidge), 3 others for the understory reiniation stage (*Tunagyna debilis* (Banks), *Pardosa uintana* and *Alopecosa aculeata*) and 2 for the old-growth stage (*Ceratinella buna* Chamberlin and *Gnaphosa microps*) (Figure 2.4).

2.4.3 Comparison of natural versus managed stands

I observed differences in spider assemblages between cut and uncut stands using NMDS ordination (Figure 2.5; stress = 13.33). In one sector (Cramolet), axis 1 reflected a gradient of increasing intensity of harvesting: partial cuts with

increased retention (66%) maintained spider assemblages that were closer to control stands (100% retention) than did partial cuts with lower retention (33% retention) or CPRS (0%). Spider assemblages in the three other sectors (Fénélon, Gaudet and Puiseaux: all old-growth prior to cutting) responded similarly to cutting treatments and appeared to show less variability within each sector. Compared to uncut stands, spider assemblages in these cut stands were more similar to old-growth stands but still fell outside the range of natural variability.

When all cut and uncut stands were included in the dbMRT (Figure 2.6), the effects of harvesting on the spider assemblages observed in the NMDS was corroborated. However, prediction of the coarse filter approach whereby partial cuts were expected to be more similar to old-growth was not confirmed. The dbMRT explained 79.8% of the variation (Figure 2.6) (cross-validated error = 0.593 ± 0.129) and was chosen 599 out of 1000 times. I observed an interaction between harvesting and stand age which was important for distinguishing old-growth, understory reinitiation and stem exclusion stages. Stands were initially divided based on stand age into those greater than116.5 years old. Following this initial split, we observed a strong sector effect where both cut and uncut stands from the younger Cramolet sector (ca 100 years before cut) were then grouped in a single terminal node. Eight species (*Bathyphantes pallidus* (Banks), *Antistea brunnea* (Emerton), *Centromerus longibulbus* (Emerton), *Callobius bennetti* (Blackwall), *Pirata cantralli* Wallace & Exline, *Xysticus emertoni* Keyserling, *Grammonota gigas* (Banks) and *Tapinocyba simplex* (Emerton)) showed strong affinity for the Cramolet site (Figure 2.6). Three other species (*Pirata montanus* Emerton, *Xysticus canadensis* Gertsch and *Clubiona canadensis* Emerton) were associated with the two other uncut stem-exclusion stands (Figure 2.6). Among sites older than 116.5 years, stands were divided into cut and uncut stands. No older, cut stand exceeded 7.24 $m^2 \cdot ha^{-1}$ in basal area (45% retention). This is in comparison to older uncut stands which had at least 13.32 $m^2 \cdot ha^{-1}$ basal area. Thus, treated stands of the Fénélon, Gaudet and Puiseaux sectors formed a single terminal node with 9 associated species (*Pardosa xerampelina* (Keyserling), *Gnaphosa muscorum* L. Koch, *Ceratinella buna* Chamberlin, *Drassodes*

neglectus (Keyserling), *Zelotes puritanus* Chamberlin, *Micaria aenea* Thorell, *Neoantistea agilis* (Keyserling), *Ceratinopsis labradorensis* Emerton and *Ozyptila sincera canadensis* Dondale & Redner). The remaining uncut stands were then resolved into two groups based to their age (158.5), and conformed to Harper's model (2005) between old-growth and understory reinitiation stages. One species, *Grammonota angusta* Dondale, was associated with the understory reinitiation stands while *Tunagyna debilis* (Banks), *Pardosa uintana* Gertsch and *Alopecosa aculeata* (Clerck) were no longer associated with this stage (contrary to what I observed in previous analyses when only uncut stands were included). *A. aculeata* was now favoured by cutting and was now more associated with cut the group of cut old-growth stands (IndVal = 35%, $p< 0.001$). This was also the case for *Gnaphosa microps* (IndVal = 39%, $p< 0.001$) and *Ceratinella buna* (IndVal = 59%, $p< 0.001$), which were previously associated with the uncut old-growth stage. *Pardosa mackenziana* was more widely distributed between stands, but also showed greater affinity for cut old-growth stands (IndVal = 0.30, $p<0.05$). A smaller 4 leaved tree (not shown) differed from the 5 leaved tree only by regrouping all uncut stands that are 133 years or older. This smaller tree was only weakly supported (306 times out of 1000) and only *Pocadicnemis americana* showed significant affinity for this larger group (IndVal = 0.49, $p=0.04995$).

Again, differences in spider assemblages among cut and uncut stands were linearly related to differences in basal area (Mantel test: $r = 0.557$, $p< 0.001$) and to a lesser extent to stand age (prior to cutting for treated stands) (Mantel test: $r = 0.393$, $p< 0.001$) (Table 2.1). Changes in other variables related to age of the stands, namely basal area prior to cutting (Mantel $r = 0.374$, $p < 0.001$) and organic matter thickness (Mantel $r = 0.267$, $p = 0.003$) were also linearly related to changes in spider assemblages. Additional variables related to cutting namely retention percentage (Mantel $r = 0.417$, $p< 0.001$) and time since the last disturbance (Mantel $r = 0.220$, $p = 0.012$) were also linearly related to changes in spiders assemblages.

Individual species showed strong affinities for cut stands independently of stand age prior to cutting. This was most apparent for *Pardosa moesta*, which

was also the most abundant species in our study, with only 7 (0.56%) specimens captured in uncut forests compared to 1242 (99.44%) captured in cut stands. However, in partial cuts with higher retention at Cramolet, only 3 specimens were found. This was similar to the maximal abundance of *P. moesta* found in uncut forests (4 in 185 year old stand). The second lowest number of *P. moesta* in a treated stand was 29 (Gaudet higher retention, see Annex). Another but less abundant species, *Pardosa fuscula* (Thorell) was also largely more abundant in cut stands (42 of 43 individuals).

2.5 Discussion

Stand basal area had a strong effect on spider assemblages both in harvested and uncut stands. This suggests that coarse filter management based on basal area and retention – a cohort model including partial cuts – could be used as a valuable management tool for conserving biodiversity but only if the amount of basal area left in treated stands is consistent with the basal area of the emulated stands. In the RECPA, the reduction in basal area following harvesting resulted in an invasion of open habitat specialists, which has been observed elsewhere (Buddle *et al.*, 2000; Larrivée *et al.*, 2005; Pearce *et al.*, 2004). Among species invading clearcuts, *Pardosa moesta* is a recurrent species showing drastic increases after treatment (Buddle *et al.*, 2000; Larrivée *et al.*, 2005; Pearce *et al.*, 2004) that was almost absent from our uncut stands. Given the level of harvesting in Canada, this could be one of the animals that are experiencing massive changes in abundance nationwide. Ecological impact of a relatively small but abundant predator like *P. moesta* may not be negligeable as large-scale deforestation occurs. Smaller organisms usually associated with forested habitats like Linyphiidae may suffer the most on the long-term from the double effect of deforestation and invasion by bigger predators like this.

In old uncut forests, prolonged absence of fire (stand age > 158.5 years) favoured spider assemblages that were different but more representative of open habitats. Stand age is strongly correlated to moss thickness and basal area (Fenton *et al.*, 2005) and the interaction of these factors provides an example of how

reduction of basal area from paludification and cutting can have an effect on biodiversity. The mantel test better captured the linear relationship between changes in basal area and spider assemblages, while dbMRT highlighted stages of stand development consistent with Harper's model (2005). We view the complementarity in these analyses as an eloquent concordance between constrained (dbMRT and Mantel tests) and unconstrained (NMDS) analyses and as corroboration that the most important explanatory variables have been measured.

Site differences were also apparent in our study, especially for spider assemblages in Cramolet. These differences in spider assemblage can in part be attributed to conditions existing in stands prior to treatment. As shown in the dbMRT, Cramolet stands were younger before cut (100 years old) than in the other sectors (183 years old or more) and did not contain spider assemblages consistent with the other sectors prior to cutting. This may be a result of a pre-treatment recruitment effect (Work, 2010). The pre-treatment recruitment effect may still be important at Cramolet especially because spiders were collected only 0-1 years after harvesting compared to other sectors which were harvested 3-5 years after cut in the other sectors. It is possible that species assemblages at Cramolet are still responding to the initial effects of cutting as is often observed (Buddle *et al.*, 2006; Jacobs *et al.*, 2008; Matveinen-Huju and Koivula, 2008; Saint-Germain *et al.*, 2005). For example, other taxa such as ground-beetles (Coleoptera: Carabidae) have been shown to maintain dwindling populations of forest specialists 1-2 years after cutting and to recruit open habitat and generalist species at the same time (Jacobs *et al.*, 2008; Niemelä *et al.*, 1993; Spence *et al.*, 1996). Similar responses could be occurring within spider assemblages (Buddle *et al.*, 2006). Alternatively, differences at Cramolet could also be attributed to geographic differences as this site is *ca.* 100 km away from the other sectors. Currently, I am unable to distinguish between these possibilities. Cramolet is also interesting because the remnant basal area in partial cuts in this sector (minimum 16.57 m^2/ha) is higher than in any other sector and nearer to what is found in old natural stands. Moreover, these results are consistent with other studies in the

boreal that effects of harvesting on spider assemblages are largely proportional to harvesting intensity (Matveinen-Huju and Koivula, 2008; review by Pearce and Venier, 2006).

Based on sectors other than Cramolet, it is clear that partial cutting in stands that were 183 years old or older did not favour spider assemblages associated with old-growth stands. Instead, partial cutting in this context had effects similar to CPRS and created assemblages that have no obvious natural analog. This result supports one of the basic assumptions of the coarse filter approach – that we have to maintain or emulate natural habitats – as partial cutting in these old sectors left only 7.24 m^2/ha in basal area, well below the minimum value of 13.32 m^2/ha seen in our uncut reference stands. Low basal areas outside the range of natural variability and assemblages with no natural analog suggest that partial cutting in old and paludified stands is not adequate to recreate or maintain old forest attributes (Bergeron *et al.*, 2007). Knowing that partial cutting and CPRS can promote paludification in these stands (Lavoie *et al.*, 2005a, 2005b) and that basal area was greatly reduced by harvesting, it is possible that cutting generated attributes and spider assemblages more representative of excessively old stands such as stands with advanced paludification or bogs.

While I can easily assert that cutting changed old-growth spider assemblages by promoting open habitat species and certain generalists, it is difficult to identify negative effects on specific species, as no species were uniquely associated with old-growth stage. Pajunen *et al.* (1995) observed a similar lack of old growth specialist spiders in southern Finland. In my study area, lack of compositional differences in dominant tree species during later stages may explain in large part the lack of spider species associated with old stands (Paquin et Coderre, 1997). In other ecosystems, such as the boreal mixedwood, where succession consists of a gradual turnover in tree species and subsequent leaf litter, arthropod assemblages may vary according to stand development due to associated changes at the ground level (Paquin et Coderre, 1997). In our sites, changes at the ground level occur without tree species turnovers and originate from natural canopy opening associated with decreasing basal area and paludification (Fenton *et al.*, 2005;

Lavoie *et al.*, 2005a, 2005b). In old stands, light availability can be 3 times higher than in young stands (Fenton and Bergeron, 2006) and could possibly facilitate mobile, visual hunters such as the Lycosid and Gnaphosid species associated both to cut and uncut old stands (*Alopecosa aculeata* and *Gnaphosa microps*). . Increased light penetration may also facilitate development of spiderlings through the sunning of egg-sacs (Pajunen *et al.*, 1995).

Drapeau *et al.* (2003) suggested that mid-successional stages of black spruce stands provide unique elements important for biodiversity of birds and attributed these benefits to the co-occurrence of structural diversity and of closed canopy and relatively high basal area. This could be also true for spiders, as earlier stages of stand development limited the presence of open-habitat species and promoted closed-canopy species. Species like *Clubiona canadensis* that directly exploit tree surfaces (Dondale and Redner, 1982) are also logically associated with closed stands with a high density of trees. Also, remnant trembling aspen trees (*Populus tremuloides* Michx) from earlier stages in mature stands may provide niche elements in younger mature stands of stem exclusion that could favour species like *Pirata montanus* that show a preference for humid deciduous litter (Paquin and Dupérré, 2003; Pearce *et al.*, 2004).

Species that are associated with forested sites tend to be in the Linyphiidae family (Pearce and Venier, 2006), but this was not observed in our study. Rather, *Ceratinella buna* and *Ceratinopsis labradorensis*, both Lyniphiidae, preferred opened stands (either old-growth stands or cut stands). It is thus possible that these species were favoured by the canopy opening and increased paludification associated with older stands, characteristics that were then exacerbated by cutting. These two species are part of generas (*Ceraticelus*, *Ceratinella*, *Ceratinopsis*, *Pelecopsis* and *Stylotector*) that are characterized by the presence of a scutum, a sclerotised part on the abdomen thought to minimize desiccation (Paquin and Dupérré, 2003), which would be an adaptation to the variable abiotic conditions in opened stands. No studies have specifically considered the role of the scutum explicitly, but our results would support a hypothesis that this could be a useful adaptation in dryer environments.

2.6 Conclusion

My study highlights the challenges of implementing partial cutting in old stands as prescribed by the cohort model. Old stands with an already reduced basal area and thicker organic layer may be particularly sensitive to additional reductions of basal area from partial cutting and thus harbor spider assemblages that have no natural analogue.

However, partial cutting may still have the potential to emulate old stands if it is implemented in mature productive stands to be consistent with the widely proposed but poorly tested coarse filter approach for conservation. To resolve these issues, future investigations should concentrate on understanding responses of arthropod assemblages in partial cuts with higher levels of retention in mature and older stands and track changes in arthropod composition over longer timeframes. Basal area was highly determinant of spider assemblages and the same could be true for other biodiversity components. Basal area retained after partial cutting should thus conform to the range of natural variability with particular attention to age of the stand prior to cutting if we hope success of this practice to preserve biodiversity associated with old-growth stands.

Table 2.1 Mantel test results (r = Mantel statistic based on Pearson's product-moment correlation) of changes in spider assemblages related to changes in stand descriptive variables. CWM = downed coarse woody material

	Uncut stands r	All stands (cut and uncut) r
Actual basal area ($m^2 \cdot ha^{-1}$)	0.5671***	0.5571***
Time since the last fire (or TSF, years)	0.3744**	0.3927***
Organic matter (cm)[§]	0.4510**	0.2669**
Volume of CWM[£] ($m^3 \cdot ha^{-1}$) Total	0.1290	0.0133
Decay class 1	0.0452	0.1095
Decay class 2	-0.0006	0.0031
Decay class 3	0.1368	0.0747
Decay class 4	0.0081	-0.0876
Decay class 5	-0.0197	-0.0719
Basal area ($m^2 \cdot ha^{-1}$) prior to cutting	(same as actual)	0.3739***
Time since the last disturbance (years)	(same as TSF)	0.2199*
Retention (%)	(impossible, all 100%)	0.4166***

[§] analyses with O.M. do not include POP

[£] analyses with CWM do not include Fénélon Control

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

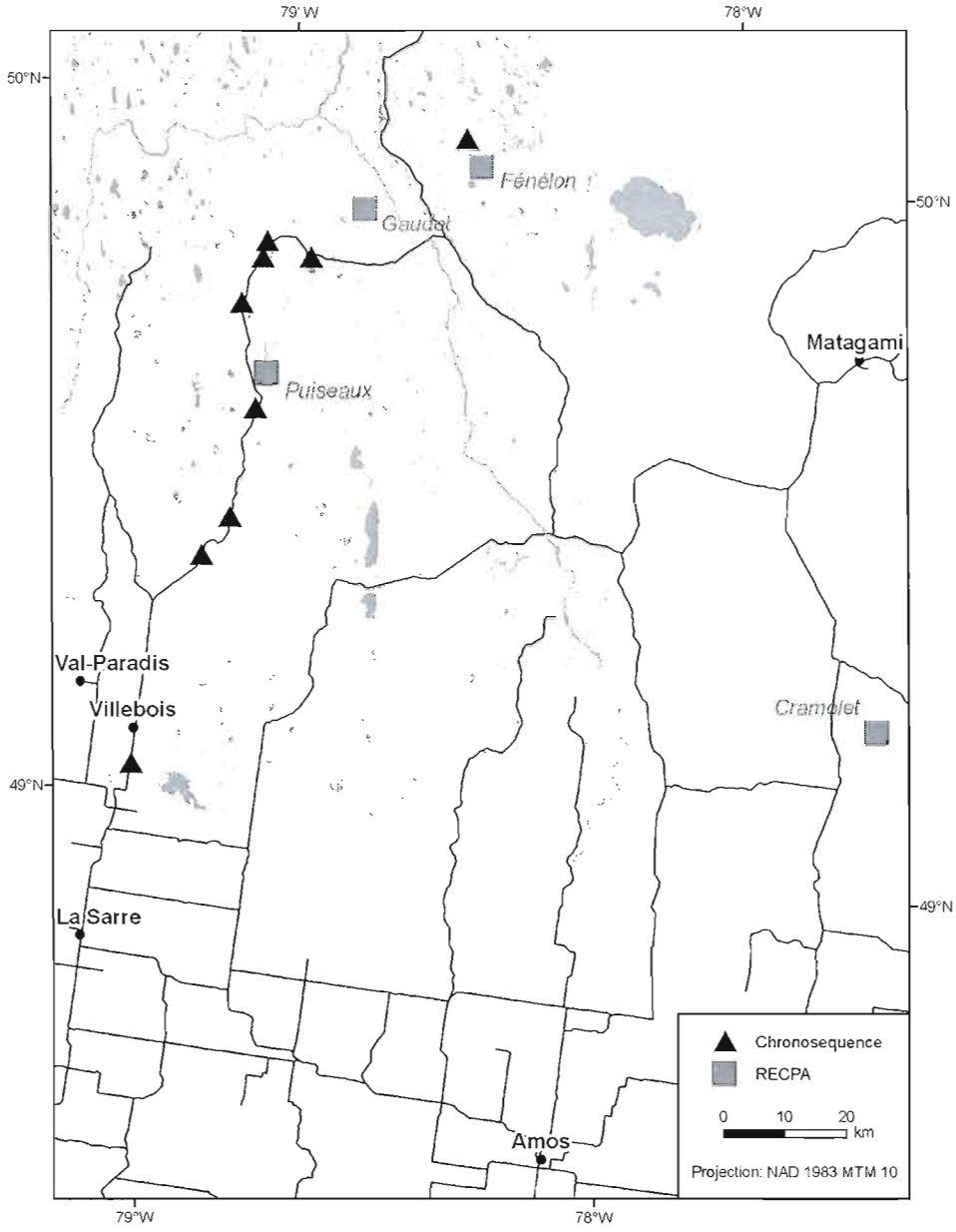

Figure 2.1 Map of the study area.

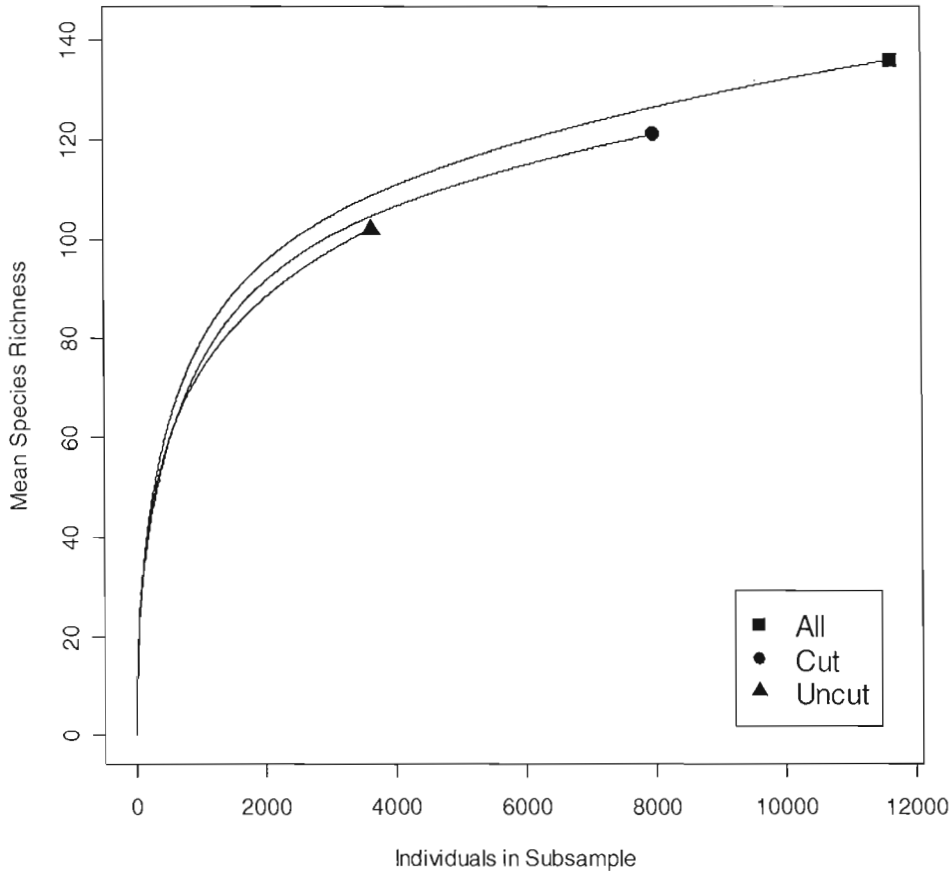

Figure 2.2 Individual based rarefaction curves for uncut stands, cut stands and all stands combined.

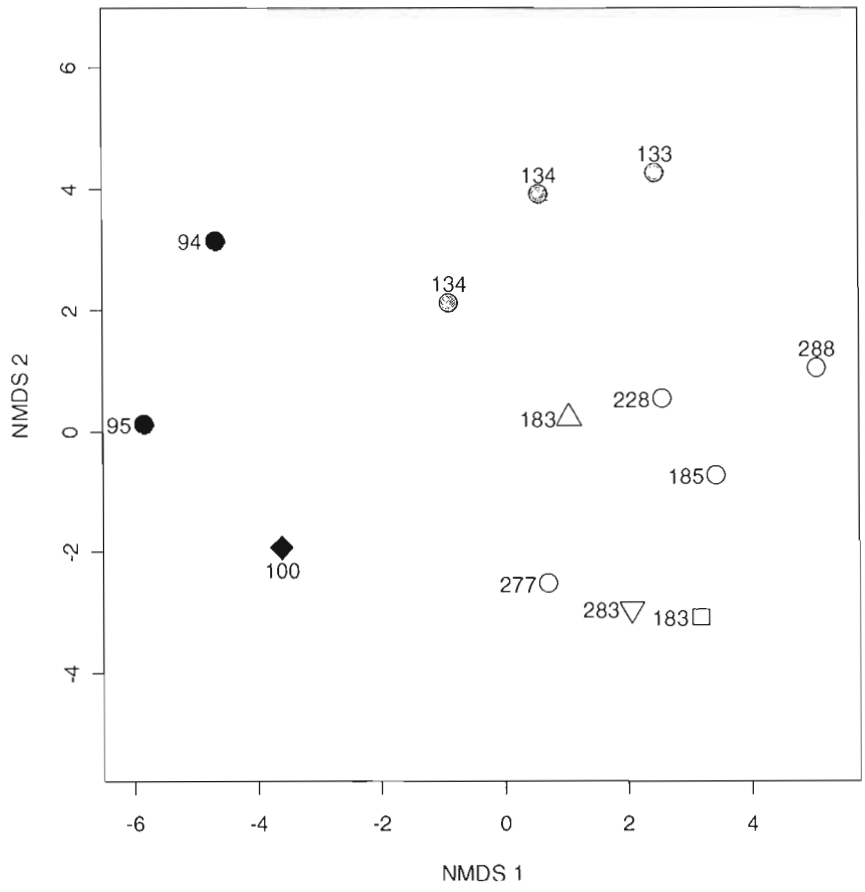

Figure 2.3 NMDS (stress = 11.20) of uncut stands (numbers are their age) based on spider assemblages (3648 individuals). Circles represent the chronosequence stands and polygons each represent a different control stand of the RECPA. Diamond = Cramolet; Triangle point up = Fénélon, Triangle point down: Gaudet; Puiseaux = square. White = old-growth; gray = understory reinitation; black = stem exclusion.

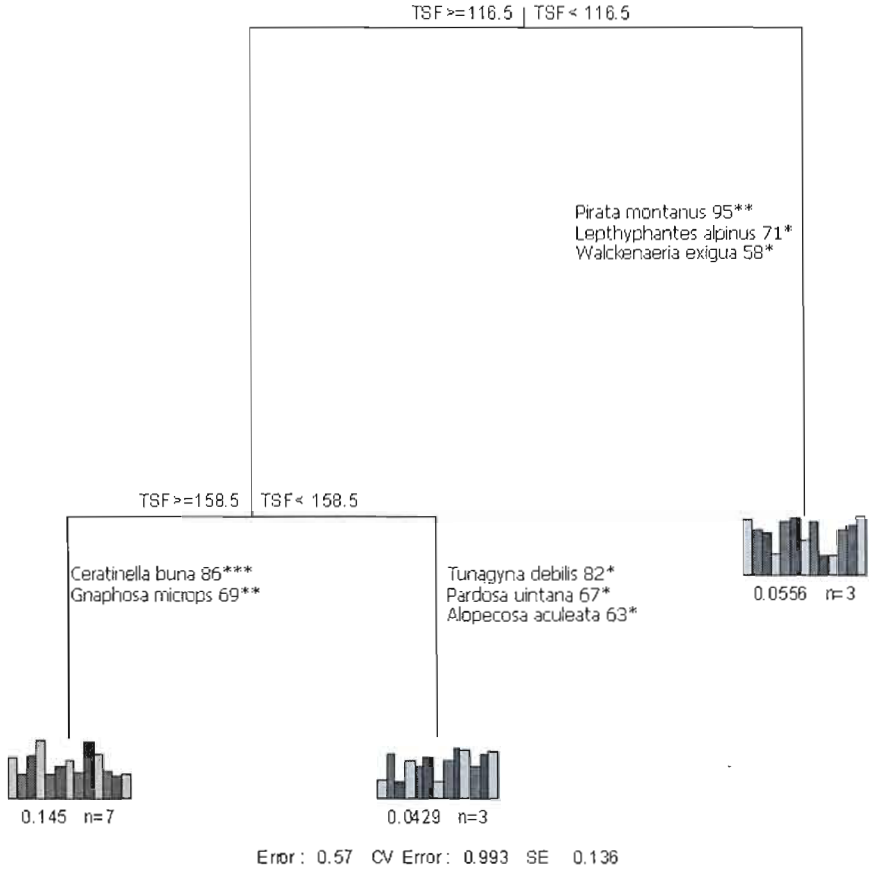

Figure 2.4 dbMRT of uncut stands based on spider assemblages regressed against stand age and structural variables (see text for more details). Indicator species are written for terminal nodes when there are.

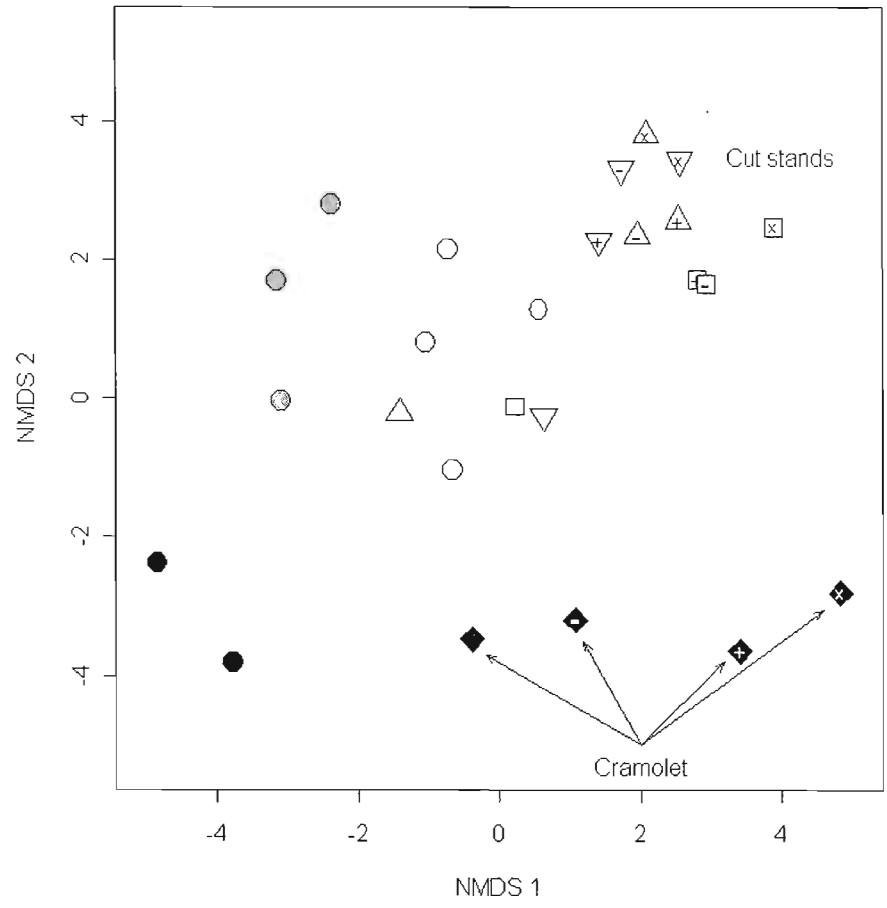

Figure 2.5 NMDS (stress = 13.33) of all stands (cut and uncut stands) based on spider assemblages (11 628 individuals). Circles represent the chronosequence stands and polygons represent RECPA sectors. Diamond = Cramolet; Triangle point up = Fénélon; Triangle point down = Gaudet; Square = Puiseaux. Color: white = old-growth; gray = understory reinitation; black = stem exclusion. Symbols: none = uncut; "-"= less intense partial cut; "+" = intense partial cut, "x" = CPRS. Note: **arrows** are used only to identify stands in Cramolet and **are not vectors** in the ordination.

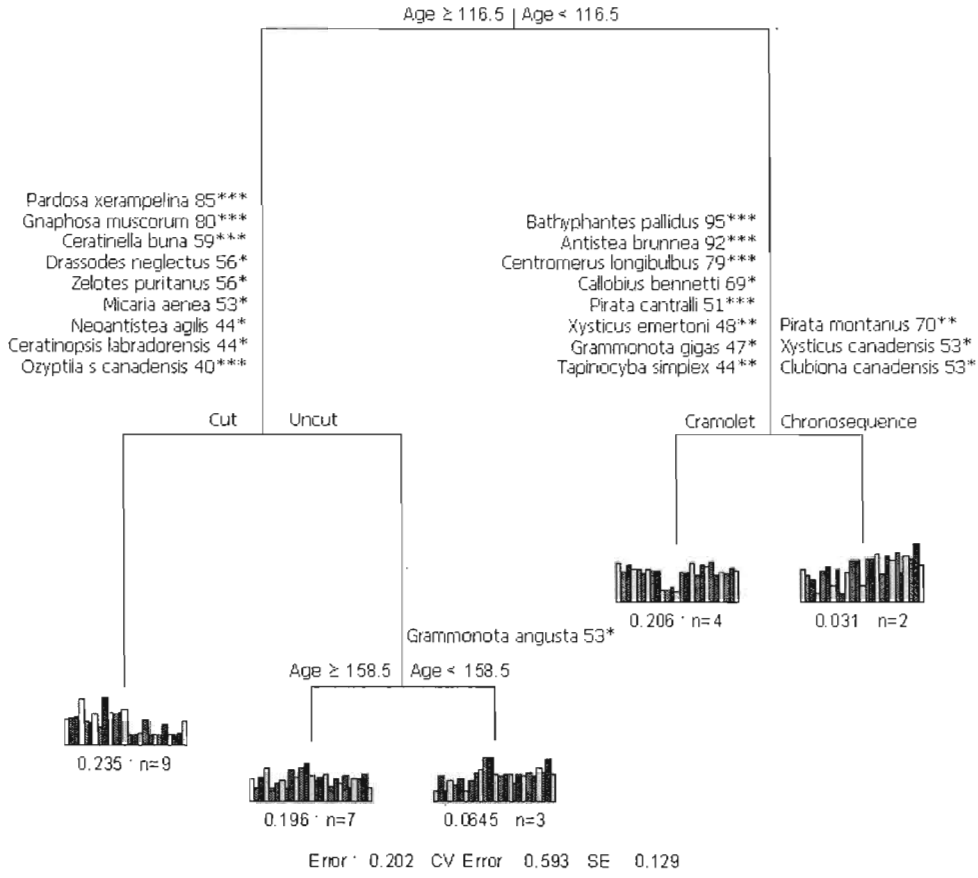

Figure 2.6 dbMRT of all stands (cut and uncut) based on spider assemblages regressed against stand age and structural variables (see text for more details). Indicator species (and their indicator value) are written for terminal nodes. Note: Ozyptila s canadensis (*Ozyptila sincera canadensis*) is the only abbreviated name for graphical purpose.

2.7 Annex

Table 2.2 Abundance of spiders in each stand
(names with scientific authorities precede)

Agelenopsis utahana (Chamberlin & Ivie); *Agroeca ornata* Banks; *Agyneta allosubtilis* Loksa, *Agyneta olivacea* (Emerton); *Agyneta simplex* Emerton; *Allomengea dentisetis* (Grube); *Alopecosa aculeata* (Clerck); *Amaurobius borealis* Emerton; *Antistea brunnea* (Emerton); *Aphileta misera* (O. P.-Cambridge); *Arctosa raptor* Kulczyn'ski, *Arctosa rubicunda* (Keyserling); *Bassaniana utahensis* (Gertsch); *Bathyphantes pallidus* (Banks); *Bathyphantes simillimus* (L. Koch); *Callobius bennetti* (Blackwall); *Carorita limnaea* (Crosby & Bishop); *Centromerus longibulbus* (Emerton); *Ceraticelus fissiceps* (O. P.-Cambridge); *Ceraticelus laetabilis* (O. P.-Cambridge); *Ceraticelus laetus* (O. P.-Cambridge); *Ceraticelus similis* (Banks); *Ceratinella brunnea* Emerton; *Ceratinella buna* Chamberlin; *Ceratinops annulipes* (Banks); *Ceratinopsis auriculata* Emerton; *Ceratinopsis labradorensis* Emerton; *Cicurina brevis* (Emerton); *Clubiona canadensis* Emerton; *Clubiona kulczynskii* Lessert; *Cnephalocotes obscurus* (Blackwall); *Cryphoeca montana* Emerton; *Cybaeopsis euopla* (Bishop & Crosby); *Cybaeopsis tibialis* (Emerton); *Diplocentria bidentata* (Emerton); *Diplocentria rectangulata* (Emerton); *Dolomedes striatus* Giebel; *Drassodes neglectus* (Keyserling); *Mermessus trilobatus* (Emerton); *Mermessus undulatus* (Emerton); *Ero canionis* Chamberlin & Ivie; *Euryopis argentea* Emerton; *Gnaphosa brumalis* Thorell; *Gnaphosa microps* Holm; *Gnaphosa muscorum* L. Koch; *Gnaphosa parvula* Banks; *Gonatium crassipalpum* Bryant; *Grammonota angusta* Dondale; *Grammonota gentilis* Banks; *Grammonota gigas* (Banks); *Hahnia cinerea* Emerton; *Haplodrassus hiemalis* (Emerton); *Haplodrassus signifer* (C. L. Koch); *Helophora insignis* (Blackwall); *Hogna frondicola* (Emerton); *Hybauchenidium cymbadentatum* (Crosby & Bishop); *Improphantes complicatus* (Emerton); *Incestophantes washingtoni* (Zorsch); *Islandiana longisetosa* (Emerton); *Lepthyphantes alpinus* (Emerton); *Lepthyphantes intricatus* (Emerton); *Micaria aenea* Thorell; *Micrargus longitarsus* (Emerton); *Microlinyphia mandibulata* (Emerton); *Microneta viaria* (Blackwall); *Neoantistea agilis* (Keyserling); *Neoantistea magna* (Keyserling); *Neon nellii* Peckham & Peckham; *Neriene clathrata* (Sundevall); *Neriene radiata* (Walckenaer); *Odeothorax trilobatus* (Banks); *Oreonetides flavescens* (Crosby); *Oreonetides vaginatus* (Thorell); *Oreophantes recurvatus* (Emerton); *Orodrassus canadensis* Platnick & Shadab; *Oryphantes aliquantulus* Paquin et Dupérré; *Ozyptila sincera canadensis* Dondale & Redner; *Pardosa fuscula* (Thorell); *Pardosa hyperborea* (Thorell); *Pardosa mackenziana* (Keyserling); *Pardosa milvina* (Hentz); *Pardosa moesta* Banks; *Pardosa uintana* Gertsch; *Pardosa xerampelina* (Keyserling); *Pelegrina flavipes* (Peckham & Peckham); *Pellenes montanus* (Emerton); *Phidippus borealis* Banks; *Pirata bryantae* Kurata; *Pirata cantralli* Wallace & Exline; *Pirata minutus* Emerton; *Pirata montanus* Emerton; *Pirata piraticus* (Clerck); *Pocadicnemis americana* Millidge; *Poeciloneta theridiformis* (Emerton); *Sciastes truncatus* (Emerton); *Scironis tarsalis* (Emerton); *Scotinotylus pallidus* (Emerton); *Sisicottus montanus* (Emerton); *Sisicus apertus* (Holm); *Sisicus penifusifer* Bishop & Crosby; *Sisis rotundus* (Emerton); *Sitticus finschii* (L. Koch); *Stemonyphantes blauveltae* Gertsch; *Styloctetor stativus* (Simon); *Tapinocyba bicarinata* (Emerton); *Tapinocyba simplex* (Emerton); *Tenuiphantes zebra* (Emerton); *hanatus formicinus* (Clerck); *Theonoe stridula* Crosby; *Theridion differens* Emerton; *Theridula emertoni* Levi; *Tibellus oblongus* (Walckenaer); *Trochosa terricola*

Thorell; *Tunagyna debilis* (Banks); *Vermontia thoracica* (Emerton); *Wabasso cacuminatus* Millidge; *Walckenaeria atrotibialis* (O. P.-Cambridge); *Walckenaeria castanea* (Emerton); *Walckenaeria communis* (Emerton); *Walckenaeria digitata* (Emerton); *Walckenaeria directa* (O. P.-Cambridge); *Walckenaeria exigua* Millidge; *Walckenaeria fallax* Millidge; *Walckenaeria lepida* (Kulczyn'ski); *Walckenaeria tibialis* (Emerton); *Walckenaeria tricornis* (Emerton); *Xysticus canadensis* Gertsch; *Xysticus ellipticus* Turnbull, Dondale & Redner; *Xysticus emertoni* Keyserling; *Xysticus luctuosus* (Blackwall); *Xysticus obscurus* Collett; *Xysticus punctatus* Keyserling; *Zelotes fratris* Chamberlin; *Zelotes puritanus* Chamberlin; *Zelotes sula* Lowrie & Gertsch; *Zornella armata* (Banks)

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Agelenopsis utahana	1	4	1	2	5	3	1	1	2	2	2	3	2	2	1	0
Agroeca ornata	5	5	1	20	7	7	9	8	4	9	4	5	5	2	3	8
Agyneta allosubtilis	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1
Agyneta olivacea	0	3	0	0	14	10	9	2	6	18	9	5	1	4	10	7
Agyneta simplex	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0	0
Allomengea dentisetis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alopecosa aculeata	2	4	7	2	63	18	14	9	24	83	39	6	27	22	17	16
Amaurobius borealis	37	7	7	19	5	9	9	5	3	5	3	3	1	3	3	2
Antistea brunnea	18	37	17	11	0	0	0	0	0	0	0	0	1	1	3	0
Aphileta misera	7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Arctosa raptor	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arctosa rubicunda	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bassaniana utahensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bathyphantes pallidus	1	6	3	4	0	0	0	0	0	0	0	0	0	0	1	0
Bathyphantes simillimus	3	6	1	1	0	0	0	2	0	0	1	2	2	0	1	8
Callobius bennetti	2	0	2	5	0	0	0	0	1	0	0	0	0	0	0	0
Carorita limnaea	0	2	0	1	0	1	2	2	0	0	0	1	1	0	1	1
Centromerus longibulbus	2	10	4	2	0	1	0	0	0	0	0	1	3	0	1	0
Ceraticelus fissiceps	1	0	1	2	0	0	1	2	0	0	0	2	0	1	0	0
Ceraticelus laetabilis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ceraticelus laetus	0	0	10	0	0	0	0	0	0	0	0	4	0	0	0	0
Ceraticelus similis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratinella brunnea	0	0	0	0	2	0	0	0	1	0	0	0	2	0	1	0
Ceratinella buna	0	1	1	0	5	15	15	0	13	16	16	2	6	10	7	2
Ceratinops annulipes	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0
Ceratinopsis auriculata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ceratinopsis labradorensis	0	0	0	0	1	0	0	0	2	4	0	0	0	0	1	0

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Cicurina brevis	2	0	5	4	6	1	12	10	2	7	4	5	2	5	3	5
Clubiona canadensis	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Clubiona kulczynskii	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	2
Cnephalocotes obscurus	0	0	0	0	2	0	0	0	1	0	2	0	1	0	0	0
Cryphoeca montana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cybaeopsis euopla	52	60	75	45	5	15	15	18	1	16	21	17	14	11	10	19
Cybaeopsis tibialis	10	19	7	17	2	6	9	4	4	5	5	5	7	13	7	6
Diplocentria bidentata	10	16	5	19	41	25	28	11	18	25	27	21	5	7	5	30
Diplocentria rectangulata	1	6	0	1	5	0	0	1	0	0	1	0	0	0	0	2
Dolomedes striatus	1	0	3	0	0	1	1	0	0	0	0	0	0	1	2	1
Drassodes neglectus	0	0	0	0	0	0	1	0	0	1	1	0	1	2	0	0
Ero canionis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euryopis argentea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnaphosa brumalis	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Gnaphosa microps	11	9	13	9	89	60	68	10	97	111	79	48	85	75	84	34
Gnaphosa muscorum	2	0	0	0	23	1	4	0	10	18	3	1	4	3	5	1
Gnaphosa parvula	5	0	2	0	2	1	3	0	1	1	1	0	0	1	0	0
Gonatium crassipalpum	0	0	0	0	0	1	0	0	2	0	0	2	0	1	0	1
Grammonota angusta	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Grammonota gentilis	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Grammonota gigas	0	1	20	0	0	0	0	0	0	0	0	0	1	0	0	0
Hahnia cinerea	10	3	6	24	27	28	43	1	46	77	26	14	0	6	19	10
Haplodrassus hiemalis	3	0	0	0	2	1	1	1	1	1	2	0	5	3	1	0
Haplodrassus signifer	0	0	1	0	0	0	1	1	2	7	0	0	1	1	0	0
Helephora insignis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hogna frondicola	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hybauchenidium cymbadentatum	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Improphantes complicatus	1	1	0	2	3	1	3	0	2	1	1	0	2	1	4	2
Incestophantes washingtoni	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Islandiana longisetosa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lepthyphantes alpinus	1	6	0	4	0	0	0	0	0	0	0	2	0	0	0	0
Lepthyphantes intricatus	0	3	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Mermessus trilobatus	0	0	0	0	8	0	1	0	0	0	0	0	0	0	0	0
Mermessus undulatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micaria aenea	0	0	0	0	3	0	0	0	5	17	1	1	1	0	2	0
Micrargus longitarsus	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Microlinyphia m. mandibulata	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microneta viaria	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Neoantistea agilis	0	0	0	0	3	1	1	0	0	0	0	0	3	0	0	0
Neoantistea magna	1	1	1	0	3	3	1	1	0	8	0	18	2	0	0	7
Neon nellii	0	1	1	3	1	2	1	1	0	4	6	3	1	2	1	1
Neriene clathrata	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Neriene radiata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Odeothorax trilobatus	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
Oreonetides flavescens	0	1	0	0	2	1	0	0	1	0	0	1	0	0	0	1
Oreonetides vaginatus	1	1	0	1	2	0	0	1	0	0	1	0	1	0	3	0
Oreophantes recurvatus	1	0	0	2	0	0	0	0	0	0	1	0	0	0	1	0
Orodrassus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oryphantes aliquantulus	1	1	0	0	1	1	1	1	2	2	1	1	1	2	0	1
Ozyptila sincera canadensis	2	5	4	2	12	16	18	10	26	20	14	5	9	4	8	5
Pardosa fuscula	35	0	0	0	0	2	4	0	0	0	0	0	1	0	0	0
Pardosa hyperborea	10	18	8	7	129	45	54	81	49	164	66	17	47	40	47	27
Pardosa mackenziana	19	20	11	13	32	23	21	10	57	56	59	11	38	34	24	1
Pardosa milvina	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Pardosa moesta	430	3	92	1	81	60	149	0	67	29	41	0	92	122	76	0
Pardosa uintana	3	12	5	1	100	38	60	12	22	87	39	20	16	14	27	13
Pardosa xerampelina	4	0	1	0	64	72	205	0	14	23	16	1	32	31	29	0
Pelegrina flavipes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pellenes montanus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Phidippus borealis	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0
Pirata bryantae	13	16	16	6	22	7	12	25	5	3	0	3	0	4	3	0
Pirata cantralli	51	113	152	77	3	16	15	19	3	20	6	21	15	11	4	25
Pirata minutus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pirata montanus	0	4	1	2	0	1	0	0	0	0	0	0	0	0	2	2
Pirata piraticus	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pocadicnemis americana	4	7	8	8	16	31	9	27	11	16	12	21	7	6	2	31
Poeciloneta theridiformis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciastes truncatus	34	8	7	32	20	21	4	22	16	16	27	14	4	9	9	20
Scironis tarsalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scotinotylus pallidus	1	1	1	1	4	0	1	0	0	1	2	3	0	1	0	0
Sisicottus montanus	1	0	0	0	0	2	0	0	1	1	0	2	0	0	0	0
Sisicus apertus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sisicus penifusifer	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sisis rotundus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitticus finschii	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Stemonyphantes blauveltae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylotector stativus	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0
Tapinocyba bicarinata	0	0	1	0	3	0	0	0	0	3	2	2	3	0	0	1
Tapinocyba simplex	5	5	1	4	4	3	4	1	1	3	0	0	1	1	6	1
Tenuiphantes zebra	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thanatus formicinus	2	0	0	0	1	1	4	0	0	1	0	0	1	0	0	0

	Cra CPRS	Cra CP-	Cra CP+	Cra Ctrl	Fen CPRS	Fen CP-	Fen CP+	Fen Ctrl	Gau CPRS	Gau CP-	Gau CP+	Gau Ctrl	Pui CPRS	Pui CP-	Pui CP+	Pui Ctrl
Theonoe stridula	0	0	1	0	0	1	0	12	2	1	0	0	0	1	0	4
Theridion differens	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Theridula emertoni	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tibellus oblongus	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Trochosa terricola	45	20	15	36	46	65	34	44	34	37	30	17	20	28	30	14
Tunagyna debilis	0	0	0	0	5	5	2	0	1	4	0	0	2	4	2	0
Vermontia thoracica	0	0	0	0	1	1	1	4	0	0	2	0	1	2	1	4
Wabasso cacuminatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Walckenaeria atrotibialis	1	4	1	1	1	10	7	1	8	2	17	5	4	0	1	12
Walckenaeria castanea	1	1	3	1	1	0	0	2	0	3	0	1	1	0	1	1
Walckenaeria communis	0	13	2	3	1	0	2	0	0	0	0	3	0	0	0	0
Walckenaeria digitata	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	1
Walckenaeria directa	0	1	0	4	0	0	0	17	1	0	2	5	0	0	0	2
Walckenaeria exigua	4	0	2	1	0	0	0	0	0	2	0	0	0	0	0	1
Walckenaeria fallax	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1
Walckenaeria lepida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Walckenaeria tibialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Walckenaeria tricornis	0	2	7	2	1	3	1	0	0	2	1	3	2	0	0	3
Xysticus canadensis	0	1	1	3	0	0	0	1	0	0	0	0	0	0	0	0
Xysticus ellipticus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Xysticus emertoni	3	4	5	2	3	4	6	1	0	2	0	0	2	1	3	0
Xysticus luctuosus	0	1	0	0	3	0	0	0	0	3	4	1	1	0	1	1
Xysticus obscurus	0	5	5	3	0	9	5	4	0	1	0	0	0	0	1	3
Xysticus punctatus	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Zelotes fratris	0	0	1	0	3	0	1	0	2	11	0	0	1	0	2	0
Zelotes puritanus	0	0	0	0	2	0	1	0	1	1	0	0	1	0	0	0
Zelotes sula	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Zornella cultrigera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

	N23 94y	S1 95y	Ch75 133y	N18 134y	N8 134y	POP 184y	N50 228y	L22 277y	N6 288y
Agelenopsis utahana	2	0	0	2	1	1	0	0	1
Agroeca ornata	18	14	13	13	26	3	9	7	4
Agyneta allosubtilis	5	0	0	0	0	0	0	0	0
Agyneta olivacea	14	0	18	4	7	13	2	3	15
Agyneta simplex	0	0	0	0	0	0	0	0	0
Allomengea dentisetis	0	0	0	0	0	0	0	0	0
Alopecosa aculeata	0	1	18	9	5	14	2	4	4
Amaurobius borealis	5	12	4	7	6	4	2	2	5
Antistea brunnea	0	0	0	0	0	0	0	0	0
Aphileta misera	0	0	0	0	0	1	0	0	0
Arctosa raptor	0	0	0	0	0	0	0	0	0
Arctosa rubicunda	0	0	0	0	0	0	0	0	0
Bassaniana utahensis	0	0	0	0	0	0	0	0	0
Bathyphantes pallidus	0	0	0	0	0	0	0	0	0
Bathyphantes simillimus	0	0	1	0	0	1	0	1	1
Callobius bennetti	0	0	0	0	0	0	0	0	0
Carorita limnaea	0	0	0	0	0	1	0	1	0
Centromerus longibulbus	0	0	0	0	0	0	0	0	0
Ceraticelus fissiceps	1	2	0	1	1	1	0	0	0
Ceraticelus laetabilis	0	0	0	0	0	0	0	0	0
Ceraticelus laetus	0	0	0	0	0	0	0	0	0
Ceraticelus similis	0	0	0	0	0	0	0	0	0
Ceratinella brunnea	0	0	0	0	0	0	0	0	0
Ceratinella buna	0	0	0	0	0	4	2	3	3
Ceratinops annulipes	0	0	0	0	0	0	0	0	0
Ceratinopsis auriculata	0	0	0	0	0	0	0	0	0
Ceratinopsis labradorensis	0	0	0	0	0	0	0	0	0
Cicurina brevis	4	2	2	4	1	9	2	6	0
Clubiona canadensis	2	3	0	0	8	0	0	0	0
Clubiona kulczynskii	0	0	0	0	1	0	0	0	1
Cnephalocotes obscurus	0	0	0	0	0	1	0	0	0
Cryphoeca montana	0	3	0	0	0	0	0	0	0
Cybaeopsis euopla	60	34	4	3	14	9	11	37	29
Cybaeopsis tibialis	4	6	0	1	2	4	5	4	6
Diplocentria bidentata	19	12	20	7	10	6	7	2	4
Diplocentria rectangulata	1	0	0	1	0	0	0	1	1
Dolomedes striatus	0	0	0	0	0	0	0	0	0
Drassodes neglectus	0	0	0	0	0	0	0	0	0
Ero canionis	0	0	0	0	0	1	0	0	0
Euryopis argentea	0	0	0	0	0	0	0	0	1
Gnaphosa brumalis	0	0	1	0	1	1	0	2	0
Gnaphosa microps	2	4	8	1	6	49	13	14	7
Gnaphosa muscorum	0	0	0	0	0	0	0	0	0
Gnaphosa parvula	0	0	0	0	0	0	0	0	0
Gonatium crassipalpum	0	0	0	0	0	1	0	1	2
Grammonota angusta	0	0	0	2	1	0	1	0	0
Grammonota gentilis	0	0	0	0	0	0	0	0	0
Grammonota gigas	0	0	0	0	0	0	0	0	0

	N23 94y	S1 95y	Ch75 133y	N18 134y	N8 134y	POP 184y	N50 228y	L22 277y	N6 288y
Hahnia cinerea	10	11	14	15	5	10	2	6	6
Haplodrassus hiemalis	1	0	0	0	0	0	0	0	3
Haplodrassus signifer	0	0	1	0	0	0	0	0	0
Helephora insignis	0	0	0	0	0	0	0	0	0
Hogna frondicola	0	0	0	0	0	0	0	0	0
Hybauchenidium cymbadentatum	1	0	0	1	0	0	0	0	0
Improphantes complicatus	2	0	5	0	2	4	0	1	1
Incestophantes washingtoni	0	0	0	0	0	0	0	0	0
Islandiana longisetosa	0	0	0	0	0	0	0	0	0
Lepthyphantes alpinus	11	7	2	2	2	0	1	0	0
Lepthyphantes intricatus	2	0	0	0	0	0	0	0	0
Mermessus trilobatus	0	0	0	0	0	0	0	0	0
Mermessus undulatus	0	0	0	0	0	0	0	0	0
Micaria aenea	0	0	0	0	0	1	0	0	0
Micrargus longitarsus	0	0	0	0	0	0	0	0	0
Microlinyphia m. mandibulata	0	0	0	0	0	0	0	0	0
Microneta viaria	0	0	0	0	0	0	0	0	0
Neoantistea agilis	0	0	0	0	0	0	0	0	0
Neoantistea magna	0	0	2	0	1	0	5	5	0
Neon nellii	1	1	0	0	0	3	0	0	0
Neriene clathrata	0	0	0	0	0	0	0	0	1
Neriene radiata	1	0	0	0	0	0	0	0	0
Odeothorax trilobatus	0	0	0	0	0	0	0	0	0
Oreonetides flavescens	0	0	0	0	0	1	0	0	0
Oreonetides vaginatus	1	1	0	0	0	0	1	5	0
Oreophantes recurvatus	1	0	0	0	0	0	0	1	0
Orodrassus canadensis	1	0	0	0	0	0	0	0	1
Oryphantes aliquantulus	1	0	1	0	2	0	3	0	2
Ozyptila sincera canadensis	0	0	4	0	2	0	4	2	1
Pardosa fuscula	0	0	0	0	0	0	0	0	1
Pardosa hyperborea	0	11	48	32	18	40	37	15	24
Pardosa mackenziana	4	5	3	10	5	10	12	10	11
Pardosa milvina	0	0	0	0	0	0	0	0	0
Pardosa mocsta	0	0	1	1	0	4	0	0	0
Pardosa uintana	1	1	50	16	22	15	18	12	19
Pardosa xerampelina	0	0	0	0	0	0	0	0	1
Pelegrina flavipes	0	0	0	0	0	0	0	0	0
Pellenes montanus	0	0	0	0	0	0	0	0	0
Phidippus borealis	0	0	0	0	0	0	0	0	0
Pirata bryantae	17	2	13	13	18	4	4	2	5
Pirata cantralli	0	5	2	0	0	7	12	3	9
Pirata minutus	0	0	0	0	0	0	0	0	0
Pirata montanus	8	28	0	0	1	0	0	1	0
Pirata piraticus	0	0	0	0	0	0	0	0	1
Pocadicnemis americana	5	0	28	4	3	9	9	18	1
Poeciloneta theridiformis	0	0	0	0	0	0	0	0	0
Sciastes truncatus	14	9	3	8	13	19	10	35	10
Scironis tarsalis	0	0	0	0	0	0	0	0	0

	N23 94y	S1 95y	Ch75 133y	N18 134y	N8 134y	POP 184y	N50 228y	L22 277y	N6 288y
Scotinotylus pallidus	0	6	0	0	0	1	0	2	0
Sisicottus montanus	5	0	1	0	3	0	2	0	0
Sisicus apertus	1	0	0	0	0	0	0	0	0
Sisicus penifusifer	0	0	0	0	0	0	0	0	0
Sisis rotundus	0	0	1	0	0	0	0	0	0
Sitticus finschii	0	0	0	0	1	0	0	0	0
Stemonyphantes blauveltae	0	0	0	0	1	0	0	0	0
Stylotector stativus	0	0	1	0	0	0	0	0	0
Tapinocyba bicarinata	0	0	0	0	0	0	0	1	2
Tapinocyba simplex	0	0	2	0	0	0	0	0	0
Tenuiphantes zebra	0	0	0	0	0	0	0	0	0
Thanatus formicinus	0	0	0	0	0	0	0	0	0
Theonoe stridula	0	0	0	0	0	0	0	1	0
Theridion differens	0	0	0	0	0	0	0	0	0
Theridula emertoni	0	0	0	0	0	0	0	0	0
Tibellus oblongus	0	0	0	0	0	0	0	0	0
Trochosa terricola	32	27	31	16	34	30	8	10	12
Tunagyna debilis	0	0	1	1	1	0	0	0	1
Vermontia thoracica	0	0	0	0	1	2	0	3	0
Wabasso cacuminatus	0	0	1	0	0	0	0	0	0
Walckenaeria atrotibialis	2	0	7	0	1	4	1	0	2
Walckenaeria castanea	2	0	1	0	1	0	0	2	0
Walckenaeria communis	1	1	1	0	0	2	0	2	0
Walckenaeria digitata	0	0	0	0	0	0	0	0	0
Walckenaeria directa	10	6	0	2	7	0	0	2	0
Walckenaeria exigua	0	1	0	0	0	0	0	0	0
Walckenaeria fallax	0	0	0	0	0	2	0	0	0
Walckenaeria lepida	0	1	0	0	0	0	0	0	0
Walckenaeria tibialis	0	0	0	0	0	1	0	0	0
Walckenaeria tricornis	0	0	0	0	0	3	0	0	1
Xysticus canadensis	4	12	2	0	5	0	0	3	0
Xysticus ellipticus	0	0	0	0	0	0	0	0	0
Xysticus emertoni	0	0	0	0	0	0	0	1	2
Xysticus luctuosus	1	0	1	1	0	0	0	0	2
Xysticus obscurus	3	1	3	1	4	1	0	0	0
Xysticus punctatus	0	0	0	0	1	0	0	0	0
Zelotes fratris	1	0	0	1	0	0	0	0	0
Zelotes puritanus	0	0	0	0	0	0	0	0	0
Zelotes sula	0	0	0	0	0	0	0	0	0
Zornella cultrigera	0	0	0	0	0	0	0	0	0

CONCLUSION

Le but ultime du travail que j'ai effectué lors de mon projet de maîtrise était d'évaluer la réponse des arthropodes à des pratiques forestières qui pourraient être employées dans un cadre d'aménagement forestier écosystémique basé sur les perturbations naturelles. Par ma collaboration avec le RECPA, ceci était surtout synonyme de déterminer si les coupes partielles pouvaient maintenir ou recréer des éléments de structure associés aux vieux peuplements pour la biodiversité en pessière noire à mousses de la ceinture d'argile. Selon le principe de conservation par filtre brut, les communautés d'arthropodes retrouvées après les coupes partielles auraient du ressembler à celles des vieux peuplements naturels si leurs habitats étaient recréés ou maintenus. Au final, les conclusions varient en fonction de quel taxon était pris en compte, et l'autocorrélation entre les différentes variables descriptives des peuplements aurait pu causer des problèmes d'interprétation des résultats mais n'a toutefois pas empêché de trouver celles qui étaient les plus importantes pour les arthropodes.

Pour les carabes, les coupes partielles et les CPRS pratiquées dans les vieux peuplements ont su garder des assemblages associés aux vieux peuplements. Dans le cas des CPRS, ceci peut sembler surprenant à cause de l'ampleur du prélèvement des tiges. Toutefois, cette pratique, tout comme les coupes partielles, conserve l'épaisse couche de matière organique accumulée avec les années sans feu. Ceci signifie donc la conservation d'un attribut forestier important pour les carabes puisque leur distribution est très influencée par les facteurs édaphiques. Les CPRS et les coupes partielles, en ouvrant la canopée du peuplement, peuvent augmenter la croissance de la mousse et la paludification dans les peuplements de la ceinture d'argile, mais ces changements n'auraient pas été notables chez les carabes étant donné que les vieux peuplements sont déjà relativement ouverts et qu'une épaisse couche de matière organique s'y était déjà formée au fil des années sans feu. Dans les peuplements plus jeunes, les effets des coupes partielles se

feraient plus sentir quelques années après la coupe et pourraient favoriser des assemblages de carabes associés aux vieux peuplements. Toutefois, il m'est impossible de le confirmer à la suite de mon projet parce que le laps de temps qui s'est écoulé entre les traitements sylvicoles qui y ont été pratiqués et l'échantillonnage des arthropodes était trop court. De plus, un seul secteur de coupe à été installé dans des peuplements plus jeunes.

Contrairement à ce qui a été observé pour les carabes, les coupes dans les vieux peuplements ont favorisé des assemblages d'araignées très différents de ceux des vieux peuplements, que ce soit par coupes partielles ou par CPRS. En effet, ces deux pratiques ont eu des effets similaires sur les assemblages d'araignées et aucun équivalent de ces traitements n'a été trouvé parmi la chronoséquence de peuplements naturels. Pour les araignées, l'importance de la surface terrière des peulements d'arbres dans la détermination de leurs assemblages a été évidente. Dans les peuplements plus jeunes, les changements après coupe étaient moins prononcés lorsque la surface terrière rémanente en arbres était plus élevée. Toutefois, un espacement dans le temps entre la coupe et la récolte des arthropodes s'avère nécessaire afin de vérifier si les coupes partielles ont pu recréer des conditions de vieux peuplements pour les araignées des peuplements matures.

Lors de futures recherches, il serait donc préférable de concentrer les efforts sur l'effet des coupes partielles dans les peuplements matures et productifs si le but souhaité est de vérifier si les coupes partielles peuvent recréer des attributs forestiers de vieux peuplements pour la biodiversité. Il serait également important que la surface terrière laissée après la coupe soit représentative de celle des peuplements que l'on souhaite recréer par une approche de filtre brut. De plus, la vraie réponse des arthropodes aux traitements est souvent décalée dans le temps et il est préférable d'attendre quelques années post-traitement avant de faire leur échantillonnage.

Néanmoins, mon projet confirme que la surface terrière des peuplements est importante dans les stratégies de conservation par filtre brut mais que le degré de paludification, l'épaisseur de la matière organique et la productivité des

peuplements qui sont inter-reliés et qui sont associés à l'âge des peuplements devraient aussi être pris en considération. Une des forces du projet est que non seulement il a été possible de comparer les assemblages d'arthropodes des peuplements coupés avec leur témoin mais aussi avec la chronoséquence de peuplements servant de référentiel naturel. Ceci a aussi permis de confirmer que la biodiversité évoluait en même temps que les peuplements et varie selon la mosaïque forestière, d'où l'importance de préserver des peuplements de tous les stades rencontrés à l'échelle du paysage pour maintenir la biodiversité.

Si notre référentiel naturel avait inclus des tourbières (l'ultime résultante de la paludification) et des peuplements affectés par des épidémies d'insectes sévères ou par des feux de faible intensité qui ne consument pas toute la matière organique et laissent une faible surface terrière d'arbres vivants, peut-être que leurs assemblages d'araignées auraient ressemblé à ceux des peuplements coupés par CPRS et coupes partielles. Toutefois, ce n'était pas le but des coupes partielles. Ainsi, le manque d'équivalent naturel d'assemblages d'araignées des peuplements coupés dans notre chronoséquence de peuplements matures et anciens supporte la suggestion que les coupes partielles pratiquées dans de vieux peuplements ne sont pas adéquates si le but visé est de recréer ou maintenir des attributs de vieilles forêts (Bergeron *et al.*, 2007).

Aucune des espèces qui ont été échantillonnées lors de mon étude ne s'est révélée être particulièrement associée aux vieux peuplements, autant chez les carabes que chez les araignées. Ceci ne signifie toutefois pas que les vieux peuplements ne sont pas importants pour ces organismes. Entre autres, les araignées de la famille des Linyphiidae sont normalement associées aux vieilles forêts mais elles ont peut-être été sous-représentées par l'échantillonnage que j'ai mené, qui se faisait à l'aide de pièges-fosses. En ce sens, la petite taille de cette famille d'araignées et la propension de certaines de ses espèces à tisser des toiles au lieu de chasser activement sont des explications plausibles, puisque ces traits limitent leur propension à tomber dans des pièges qui misent sur l'activité des organismes visés. L'exemple de *Dromius piceus*, le carabe associé aux vieilles forêts que je n'ai pas récolté dans mes pièges-fosses à cause de sa propension à

voler, appuie cette hypothèse. De plus, un échantillonnage gigantesque est souvent nécessaire et difficile à réaliser afin de récolter assez de spécimens des espèces les plus rares (qui pourraient être associées aux vieilles forêts) pour en tirer des conclusions valables scientifiquement (Martikainen and Kouki, 2003).

Pourtant, pour arriver à mes conclusions, l'identification d'un grand nombre d'arthropodes s'est avérée nécessaire, autant dans les peuplements naturels de différents âges que dans les peuplements ayant subi des traitements sylvicoles. Avant même le début du projet, j'avais déjà un vif intérêt envers les insectes et l'idée d'étudier la diversité des coléoptères terricoles m'a emballé quand Work m'a parlé du projet que j'ai accepté. Toutefois, le nombre relativement restreint de coléoptères (Carabidae et Staphylinidae) que j'ai pu récolter dans l'aire d'étude choisie n'était pas suffisant pour engendrer une étude alliant entomologie et écologie forestière satisfaisante. Work m'a donc suggéré d'inclure dans le projet d'autres arthropodes terricoles que j'avais attrapés dans mes pièges, qui étaient 10 fois plus nombreux mais qui m'intéressaient moins et que je connaissais moins : les araignées. Même si je n'étais pas très emballé par l'idée au départ, plus l'identification des spécimens et les lectures sur le sujet avançaient, plus j'étais fasciné par la diversité et la biologie de ces organismes. Aujourd'hui, je ne regrette en rien ce revirement de situation car à mon intérêt des insectes s'est ajoutée une passion et une certaine expertise des araignées.

Au final, plusieurs spécimens d'arthropodes qui ont été récoltés et identifiés ont été laissés de côté pour plusieurs raisons. Ceux qui ont été récoltés de façon préliminaire par Work et O'Connor en 2005 et 2006 et que j'ai identifiés par la suite n'ont pas été inclus dans les analyses à cause de la variabilité que cela ajoutait à mes données. En effet, seulement deux récoltes tardives ont été faites lors de l'été de 2005, alors qu'en 2006 les récoltes n'ont été faites que dans la chronoséquence et dans un seul des secteurs du RECPA dont on a tenu compte. Nous avons donc seulement gardé les années complètes (2007 et 2008). Un autre secteur, celui des collines de Muskuchii était supposé être investigué et d'ailleurs 120 pièges y ont été installés et récoltés en 2007, mais des raisons logistiques et scientifiques nous l'ont fait abandonné. En plus de son éloignement

géographique, une proportion grandissante de pièges était perturbée par des mammifères entre chaque récolte (jusqu'à plus de 80%). De plus, ce secteur était très différent des autres (sols mieux drainés, dominance du pin gris avant la récolte, traitements sylvicoles différents) et ses assemblages d'arthropodes auraient donc difficilement pu être comparés à ceux des autres secteurs du RECPA et aux peuplements de la chronoséquence. Il est également malheureux que N4, le peuplement naturel le plus jeune de la chronoséquence (54 ans), ait également du être abandonné en raison de la perturbation systématique des pièges qui y étaient installés. Au total, en comptant les années et secteurs laissés de côté, c'est donc une base de données de 2 308 carabes et 14 651 araignées qui résulte de ma maîtrise. Peut-être qu'elle pourra faire l'objet d'autres investigations dans le futur afin de répondre à d'autres questions.

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